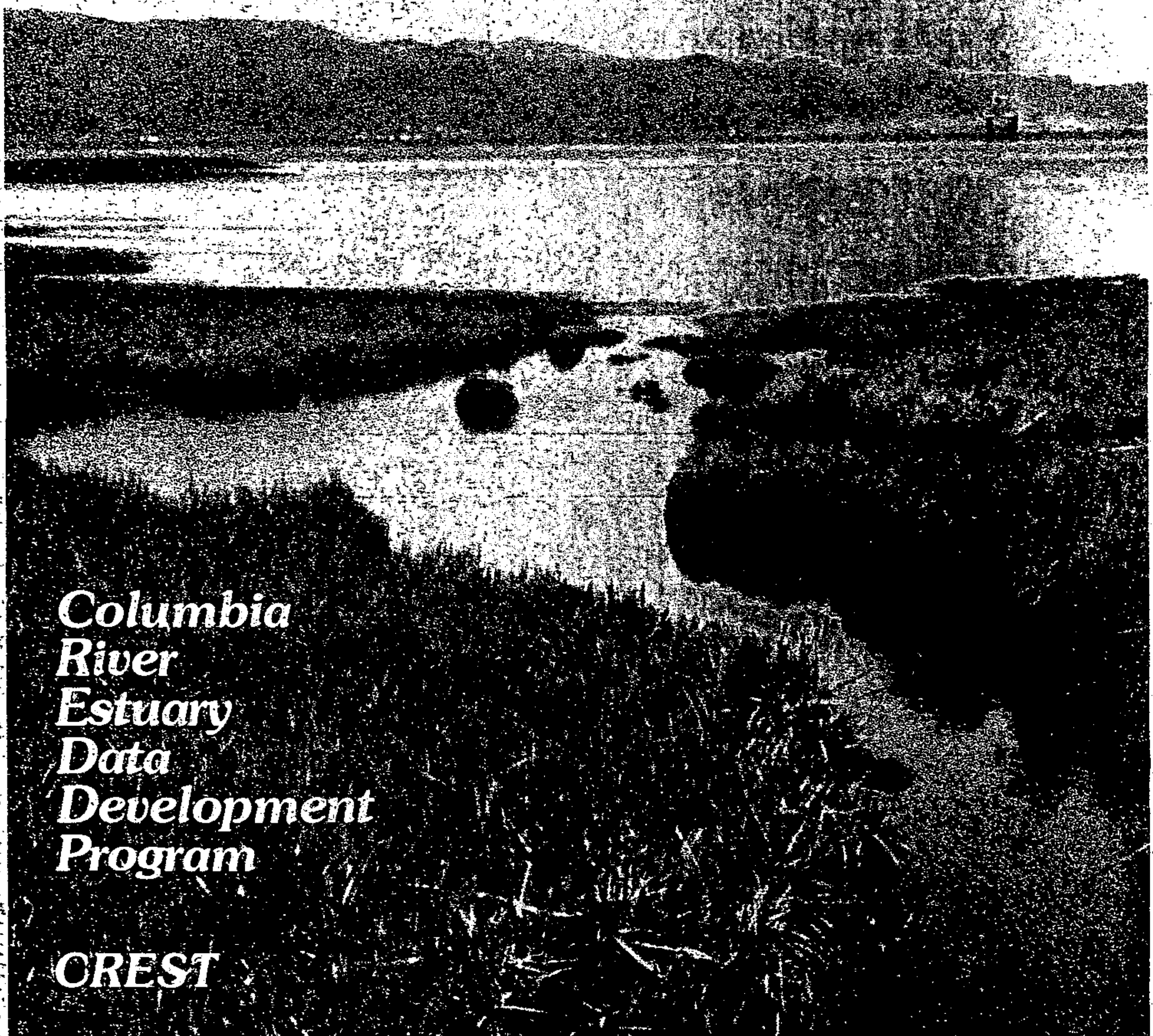
THE DYNAMICS OF THE COLUMBIA RIVER ESTUARINE ECOSYSTEM, VOLUME II



Columbia
River
Estuary
Data
Development
Program

CREST

Columbia River Estuary
Data Development Program
(CREDDP)

THE DYNAMICS OF THE COLUMBIA RIVER ESTUARINE ECOSYSTEM

VOLUME II

June 1984

THE DYNAMICS OF THE
COLUMBIA RIVER
ESTUARINE ECOSYSTEM

AUTHORS

Charles Simenstad
David Jay
C. David McIntire
Willa Nehlsen
Christopher Sherwood
Lawrence Small

WORD PROCESSING

Isabel Turner
Julie Guerrero
Elizabeth Rummell

GRAPHICS COORDINATION

Elizabeth Krebill
William Barnett

TABLE OF CONTENTS
(VOLUME II)

6. CONCEPTUAL FRAMEWORK FOR PHYSICAL-BIOLOGICAL INTEGRATION

A major goal of this report is to provide an integrated presentation of Columbia River Estuary community dynamics in relation to physical processes. This chapter presents the conceptual model used in carrying out physical-biological integration. Problems in integrating CREDDP data and considerations in model selection are described (Section 6.1). The modeling approach (Section 6.2) and details of the model itself (Section 6.3) are then presented. The model is discussed according to major biological processes: Primary Food Processes (Primary Production and Detrital Decomposition) and Consumption (Deposit Feeding, Suspension Feeding, Wetland Herbivory, and Predation).

6.1 THE PROBLEM OF INTEGRATION

Information available for integration represented many levels of biological organization and of spatial and temporal resolution. For example, the biological data included species lists, counts of organisms and estimates of densities, biomass measurements of species and groups of species, life history information about species, estimates of primary production and respiration, density and flux of organic particles in the water column, and chlorophyll concentrations in the water column and sediment. Furthermore, these data related to distributional patterns and system dynamics within a variety of temporal and spatial frames.

The major challenge in integrating CREDDP data was to develop a conceptual model that could accommodate the Program's variety of organizational frameworks and resolution levels. One possible approach was a trophic (food web) analysis of the estuarine community. In this case, estimates of production and energy inputs and outputs for all functional groups of organisms would be required. Unfortunately, such data were lacking for many of the consumer groups. Moreover, data related to complex interactions between detritus and other biological components of the system also were insufficient for a complete trophic synthesis.

For a satisfactory integration of scientific information, it also was necessary to include structural and distributional information in relationship to physical processes. CREDDP produced much data related to temporal and spatial distributions of organisms. Summaries of such data may be more relevant to certain management problems than trophic considerations, particularly problems related to the vulnerability of organisms to perturbation at specific locations.

Several conceptual models were considered for the synthesis of scientific information from CREDDP. The most notable possibilities included the Fish and Wildlife Service model from the Ecological Characterization of the Pacific Northwest Coastal Region (Proctor et. al. 1980), a trophic level model (Lindeman 1941, 1942), habitat-based model suggested by personnel of the Columbia River Estuary Study Taskforce, a hierarchical process model based on the concepts of Overton (1972, 1975, 1977) and McIntire (1983), and the hypothesis systems

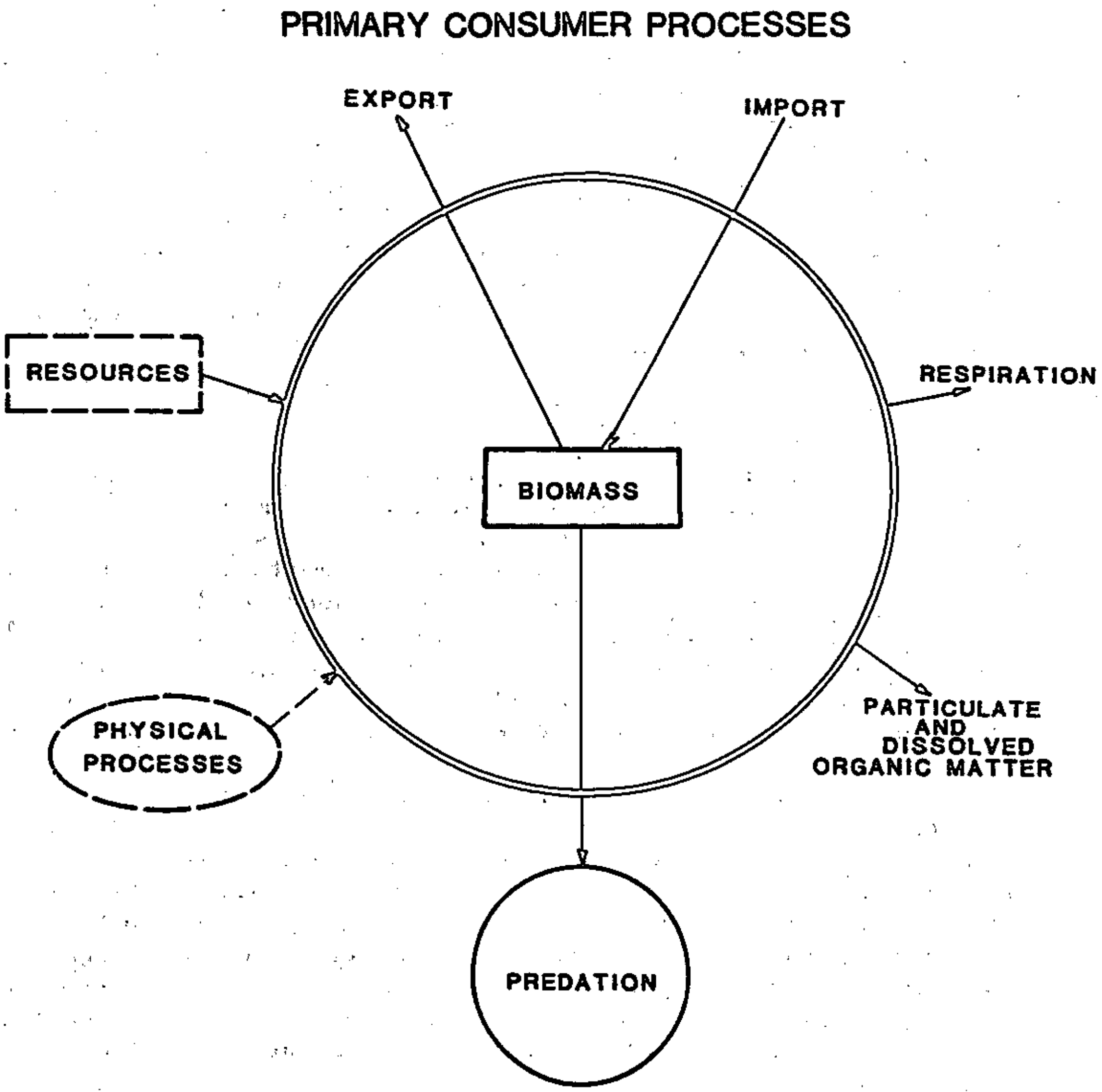


Figure 6.1. A diagram of a generalized primary consumer process illustrating its state variable and relevant input and output variables. In this case, the process of interest (large circle) is coupled to Predation, a secondary consumer process.

models introduced by the Biophysical Interactions Work Unit of CREDDP in February 1980.

The modeling approach adopted for integration was similar to that of Overton (1975) and McIntire (1983). The model, described in Section 6.2, has a hierarchical structure which accommodates the many resolution levels of the CREDDP data. Although the model emphasizes biological processes, its structure also permits consideration of important species and functional groups of species which are involved in these processes. Consequently, the model is flexible enough to organize the presentation of process dynamics in the estuary as well as information concerning distributional patterns of species. Physical processes are treated as system inputs that limit, control, or regulate biological processes.

6.2 THE PROCESS CONCEPT

The ecological literature often refers to various physical and biological processes in contexts that are usually intuitively understandable without a formal, theoretical structure. However, for analytical purposes, it is desirable to formalize the process concept by explicit definitions and the establishment of a convention for diagramming relationships. Here, the definitions apply only to biological processes; physical processes are treated conceptually as driving or control functions.

Definitions:

(1) A process is a systematic series of actions relevant to the dynamics of the system as it is conceptualized (or modeled).

(2) A state variable is a variable that represents the net accumulations of a material of interest at any instant of time.
(Examples of state variables in ecological systems are the biomasses of species or functional groups of species and the concentration of a nutrient.)

(3) A resource is any input required by a process that potentially may be in limited supply.

Figure 6.1 is a generalized diagram of a biological process. This drawing also illustrates the six symbols that will be used to diagram the individual processes that were investigated by CREDDP research projects. Biological processes are always represented by circles. A large circle is used to focus on a particular process of interest, while a smaller circle indicates another process that is coupled to the process of interest. In the case of Figure 6.1, the general structure of the featured process is compatible with a primary consumer process (e.g., grazing or deposit feeding). This process is elaborated into one state variable and other variables that represent inputs and outputs associated with the process. In this case, the state variable, illustrated by the rectangle, is the biomass at any instant of time that is involved in the process. In the system diagrams that follow, most state variables will represent biomasses of various functional groups of organisms associated with a process of interest. Other variables associated with the process in Figure 6.1 include resource inputs, imports of biomass from outside the spatial area of interest, export of biomass from the system, respiratory and waste losses generated by the process, losses of biomass to the process of predation, and the set of relevant physical variables that influence the process. In summary, biological processes are defined as those biological activities that are generated by complex interactions among a set of variables, namely the corresponding inputs, outputs and state variables.

For the synthesis of biological data from CREDDP, the problem of qualitative differences among organisms involved in a particular process is approached by partitioning the process biomass into the number of state variables that corresponds to the taxonomic entities or functional groups of organisms investigated by the various CREDDP projects. For example, biomass involved in primary production (a process) is partitioned into three state variables representing biomasses of phytoplankton, benthic algae, and vascular plants. This approach is satisfactory for the synthesis of CREDDP data, as both process and state variable dynamics receive equal emphasis within a conceptual framework familiar to the professional manager. This perspective deviates slightly from another view of process dynamics (McIntire, 1983), which ignores taxonomic categories and places the major emphasis on the capacity of a system to process inputs.

Explicit definitions for the symbols used to diagram the biological components and inter-relationships for the Columbia River Estuary are presented in Table 6.1. The approach is relatively simple, as only six symbols are used to diagram details of the various biological systems and subsystems. In addition to circles (processes) and rectangles (state variables), arrows are used to represent inputs and outputs, and the ellipse indicates physical processes that couple with the biological process of interest. If an input or output is generated by the process under consideration, it is represented by an arrow which is connected to (or originated from) the outside of the process circle. For example, the process of deposit feeding generates respiratory losses and organic waste products and actively consumes food resources (Figure 6.1). In contrast, certain inputs and outputs act directly on the state variables within a process and are not generated by the process itself. The most notable examples include biomass losses to consumer processes and imports and exports to and from the system. In other words, predators eat the biomass of organisms involved in deposit feeding, not the process of deposit feeding itself. Likewise, biomass, rather than the process, is imported or exported. Such dynamic relationships with and among state variables are represented by arrows which extend through the process circle and connect directly to the appropriate state variable. A dashed-line arrow indicates a coupling to the process of interest that does not involve transfers of matter or light energy. Relationships with physical processes are diagrammed in this way (Figure 6.1). Also, in some of the diagrams, it is convenient to distinguish between state variables within and outside the process under consideration. When this is necessary, a solid rectangle indicates a state variable within the process (i.e., the biomass involved in the process) whereas a rectangle outlined by a dashed line represents a state variable external to the process of interest.

6.3 AN ECOSYSTEM MODEL OF ESTUARINE PROCESSES

Ecosystems can be conceptualized as hierarchical systems of biological processes driven and controlled by physical and chemical processes. Depending on the resolution levels of interest, the various biological processes are the component systems, subsystems, and suprasytems. This view of ecological systems is consistent with FLEX, a general ecosystem modeling paradigm developed by W.S. Overton (1972, 1975) which is based on the general systems theory of Klir (1969).

A hierarchical model of an estuarine ecosystem is illustrated in Figure 6.2. Estuarine biological processes can be considered holistically in terms of inputs and outputs relative to the entire ecosystem. Also, Estuarine Biological Processes can be investigated mechanistically, in this case as a system of two coupled subsystems (Primary Food Processes and Consumption) that can be uncoupled and investigated holistically or mechanistically in isolation after coupling variables have been carefully identified. The Primary Food Processes subsystem represents the dynamics of variables associated with the accumulation and degradation of plant biomass and detritus, whereas the Consumption subsystem is concerned with the dynamics of macrofauna, including zooplankton, as they function as consumers of the primary food supply (i.e., living plant biomass and detritus). The subsystems of Primary Food Processes are Primary Production, which represents the production dynamics of autotrophic organisms, and Detrital Decomposition, a process that is concerned with the breakdown of dead organic material. The process of Consumption is partitioned mechanistically into four coupled subsystems: Deposit Feeding, Suspension Feeding, Wetland Herbivory, and Predation. Deposit Feeding involves the dynamics of sediment-associated macrofauna feeding on benthic food particles, while Suspension Feeding includes processes related to the removal of suspended food particles from the water column by benthic macrofauna and zooplankton. Wetland Herbivory is a process that includes the activities of terrestrial and aquatic animals feeding on the emergent plants in estuarine marshlands. Predation represents macroconsumer processes responsible for the consumption of zooplankton, deposit feeders, suspension feeders, and all herbivorous birds, mammals, and insects.

The model in Figure 6.2 illustrates estuarine processes relative to different levels of biological organization. In addition to the resolution levels of the biological components, integration of the CREDDP data had to deal with different levels of resolution relative to time. For example, system dynamics of the process of Primary Production can be investigated relative to many temporal levels of resolution (Figure 6.3). Time periods of potential interest include minutes, an hour, a day, the tidal cycle, a week, a season, and a year. In the scientific synthesis that follows, the behavioral characteristics of the systems and subsystems are reported in relationship to the temporal scales that are compatible with the data and the coupling structure of the conceptual model. In particular, outputs associated with a particular temporal level of resolution are described for specific inputs, and those outputs are interpreted relative to a longer time resolution when relevant to the dynamics of other systems. Figure

KEY TO SYMBOLS

◎	Biological process of interest
◯	Biological process that is coupled to the biological process of interest
○	Indicates relationships common to all state variables
▭	State variable internal to the process of interest
⬚	State variable (or resource) coupled to the process of interest
⬭	Physical/chemical variables controlling or affecting the process of interest
——▷	Indicates input/output of matter and/or energy
- - -▷	Indicates a coupling to the process of interest that does not involve transfer of matter nor energy

Table 6.1. Definition of symbols used to diagram the biological components and relationships for the Columbia River Estuary.

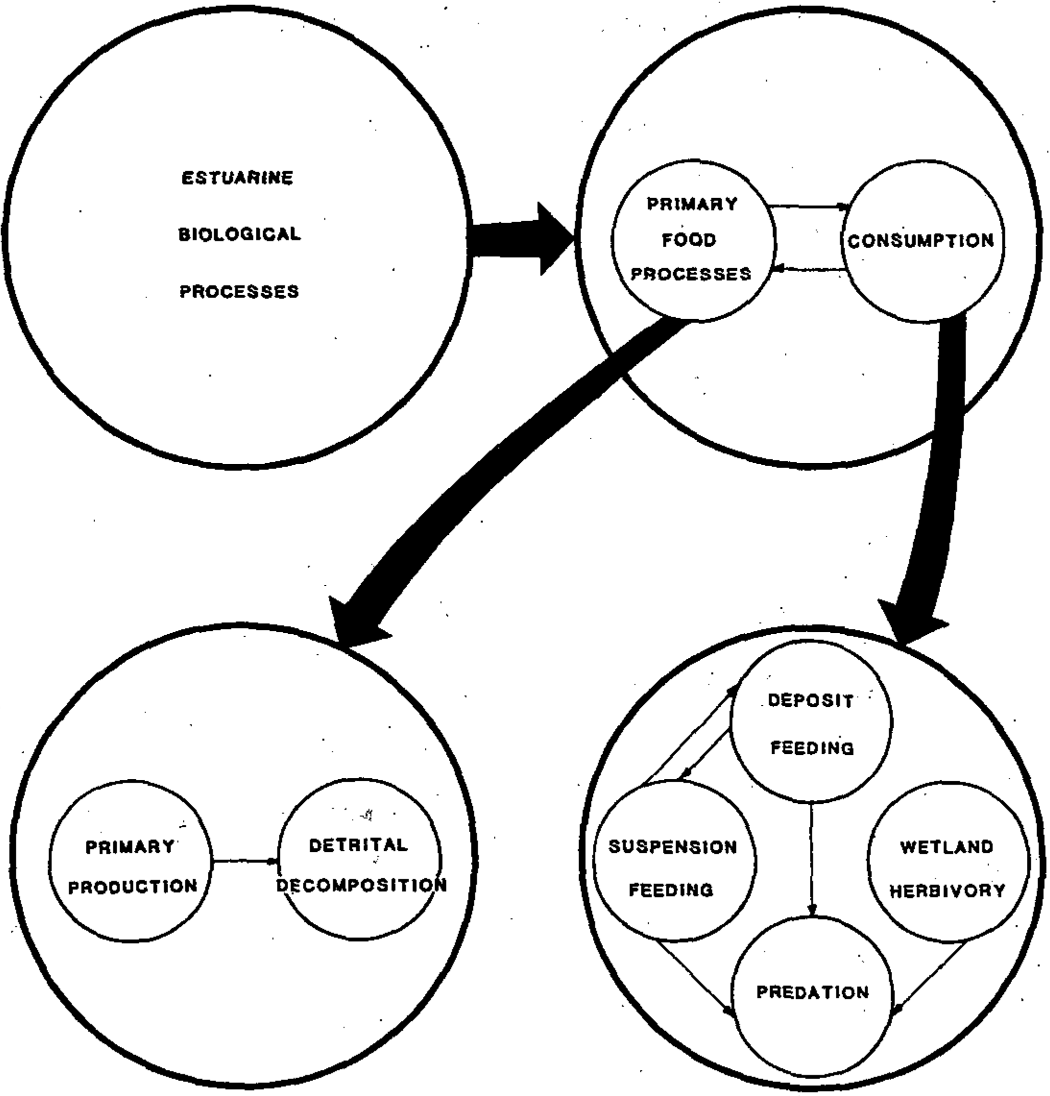


Figure 6.2. Hierarchical model of biological processes for the Columbia River Estuary. The large arrows denote the hierarchical expansion of the process from which each arrow originates. Small arrows indicate the existence of coupling variables linking the processes joined by the arrows.

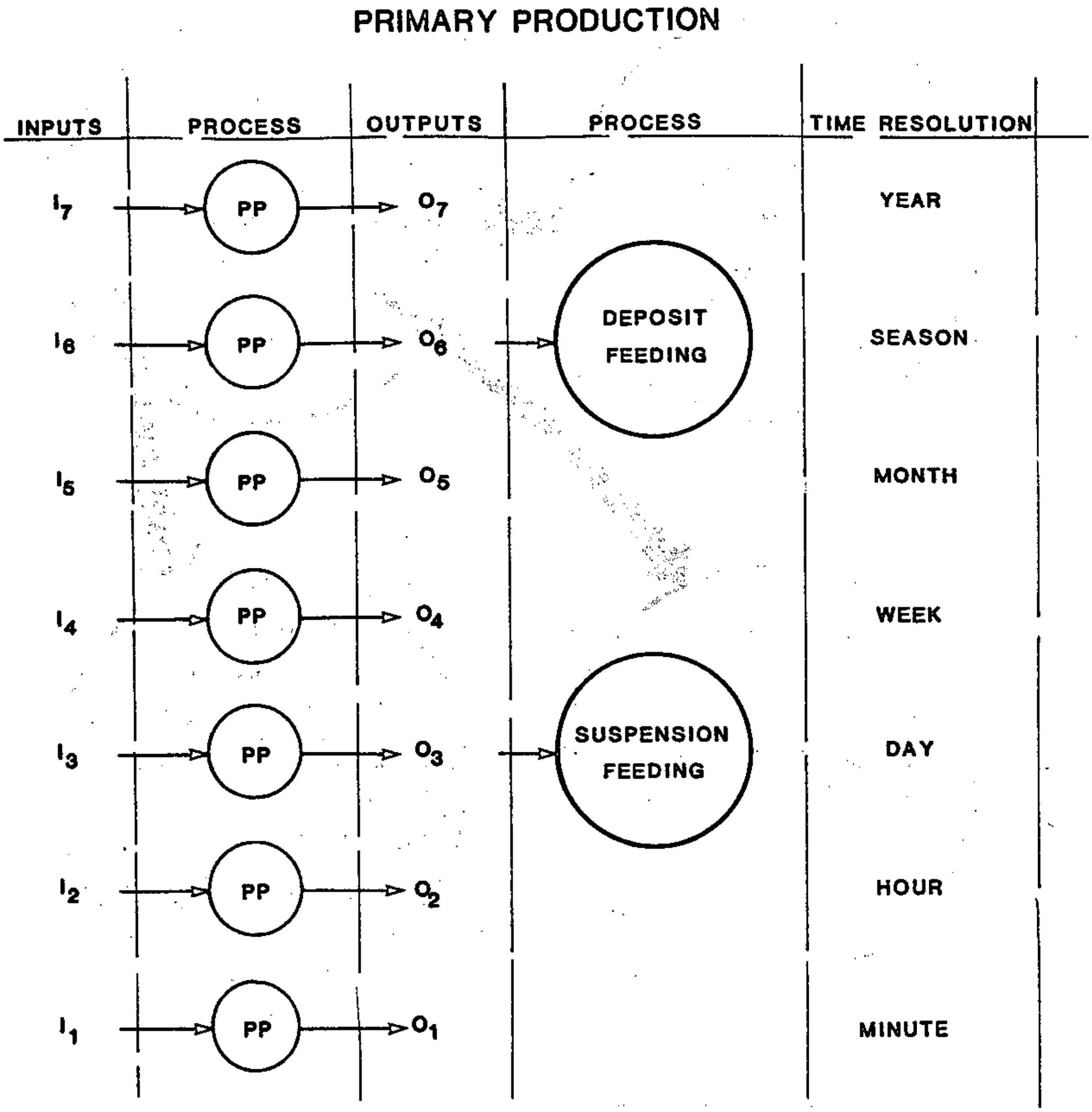


Figure 6.3. A diagram of the Primary Production (PP) subsystem, illustrating system dynamics at different temporal levels of resolution. The levels relevant to the process of Deposit Feeding and Suspension Feeding are indicated as season and day, respectively.

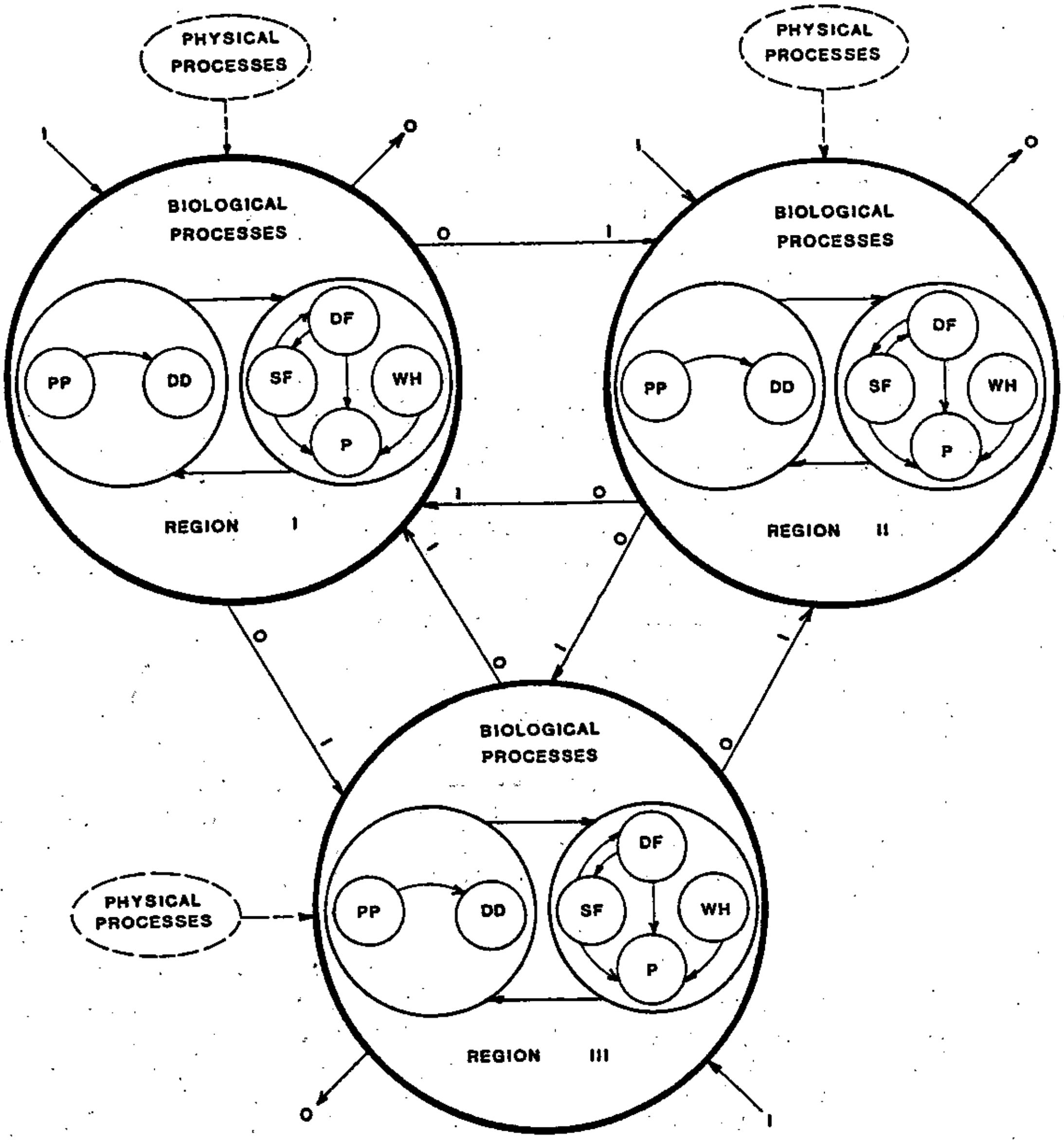


Figure 6.4. A diagram illustrating process dynamics for selected regions of interest. In this case, some outputs (O) from one region are inputs (I) to other regions. Biological processes are conceptualized as the structure presented in Figure 6.2, where the fine resolution processes are Primary Production (PP), Detrital Decomposition (DD), Deposit Feeding (DF), Suspension Feeding (SF), Wetland Herbivory (WH), and Predation (P).

6.3 illustrates this concept by indicating the temporal levels of resolution that are relevant to the dynamics of two consumer processes relative to the outputs from the Primary Production subsystem. The diagram suggests that the dynamics of Deposit Feeding and Suspension Feeding by zooplankton operate on a seasonal and daily time resolution, respectively, relative to the dynamics of the process of Primary Production. In other words, output 0_6 (season) operates on a time scale that is adequate to predict the dynamics of Deposit Feeding, in relation to Primary Production, whereas output 0_3 (day) is necessary to understand the dynamics of Suspension Feeding by zooplankton.

The problem of spatial variation in the Columbia River Estuary is approached conceptually by examining the dynamics of the biological processes relative to inputs that are specific for the spatial areas under investigation. These inputs include physical and chemical driving variables as well as various biological couplings with adjacent regions (Figure 6.4). Biological processes within the defined spatial boundary simply respond in a way that is compatible with the inputs. Therefore, these processes may turn off and on or modify their dynamics as the spatial resolution and area of interest changes. For example, as interest shifts from tidal flats to the water column, the process of Deposit Feeding becomes inoperative, while Suspension Feeding may assume a major role in system dynamics. However, at a different level of resolution, the process of Consumption operates in both spatial regions, because both Deposit Feeding and Suspension Feeding are subsystems of Consumption (Figure 6.2). For integration of the CREDDP scientific information, the estuary is partitioned into regions and habitat types that are relevant to ecological considerations and some current management objectives, and compatible with the structure of the CREDDP data base.

Figure 6.2 presents the general hierarchical structure of the conceptual model for integration, but does not illustrate the detailed structure and relationships for the individual processes and subprocesses. Such details are discussed and illustrated in the following sections according to the convention introduced in Figure 6.1 and Table 6.1. Estuarine Biological Processes are partitioned into two subsystems, Primary Food Processes and Consumption, and the structures of these subsystems are described relative to inputs, outputs, and relevant state variables. Primary Food Processes and Consumption then are partitioned further, and their subsystems are discussed in relation to corresponding inputs, outputs, state variables, and couplings with other subsystems.

6.3.1 Primary Food Processes

Primary Food Processes are biological processes concerned with the accumulation of plant and detrital biomass (Figure 6.5). Resources for this system include light energy and nutrients. Since the inputs of these resources are generated by the biochemical processes of photosynthesis and nutrient uptake, the couplings are indicated by arrows between the rectangles and the perimeter of the process circle. Process-generated outputs from the Primary Food Processes system include respiratory losses and losses of dissolved organic matter which result from the metabolic activities of autotrophic organisms and heterotrophic microorganisms. At this level of resolution, the internal state variable is the Primary Food Supply which represents the combined biomasses of autotrophic organisms and detritus with associated microorganisms. The Primary Food Supply is a resource for a variety of consumer organisms, some of which do not discriminate between the autotrophic and detrital components of this state variable. Photosynthesis and nutrient uptake are the principal sources of autotrophic biomass, while detrital accumulation depends on imports from outside the region of interest, on inputs derived from the outputs of other processes, and on the internal, within-process transfer of organic matter which occurs after the natural mortality of autotrophic organisms. In addition, nutrients are pumped into the system by heterotrophic microorganisms involved in the decomposition of the Primary Food Supply. The inputs to the detrital component of the Primary Food Supply are indicated by arrows to the rectangle inside the circle, as they represent a transfer of organic matter from outside the process which is coupled directly to a state variable. For example, the coupling from Consumption to the Primary Food Supply indicates the transfer of non-living organic matter, both as fecal discharge and dead organisms, from the consumer functional groups to the state variable of the Primary Food Processes subsystem. Export of biomass from the Primary Food Supply is represented by an arrow originating from the state variable and extending outside the process circle. Such exports affect the state variables directly, and are often controlled by physical factors external to the process. Consumption of the Primary Food Supply is indicated by an arrow extending from the internal state variable to the process of Consumption.

6.3.2 Subsystems of Primary Food Processes

Although some scientific and management questions relate directly to the holistic behavior of the Primary Food Processes subsystem, other questions may require a more detailed, mechanistic examination of this subsystem. For our purposes, Primary Food Processes is investigated mechanistically relative to two subsystems: Primary Production and Detrital Decomposition (Figure 6.2). This structure partitions a process that received major emphasis by three CREDDP research units (Primary Production) from a process that received relatively little attention in the program (Detrital Decomposition). CREDDP projects with the Primary Food Processes subsystem are described by Macdonald and Winfield (1984), McIntire and Amspoker (1984) and Frey et al. (1984). The major coupling variable between Primary Production and Detrital Decomposition is the transfer of dead plant material from the state variables that represent living plant biomass to Detritus, the state variable of Detrital Decomposition.

Primary Production

Process-generated input and output variables for the Primary Production subsystem are th same as those described for the Primary Food Processes subsystem (Figures 6.5 and 6.6). However, in the case of the Primary Production subsystem, losses of dissolved organic matter and respiratory energy are confined to outputs from living plant material only. State variables associated with Primary Production include Phytoplankton, Benthic Algae, and Vascular Plants. The relative importance of these functional groups obviously depends on the spatial area under investigation. Outputs common to all state variables (i.e., losses to Detritus, Export, and Consumption) are diagrammed by arrows extending from a central node to the appropriate process or variable in order to reduce the number of arrows used in Figure 6.6. Since many microalgae are both planktonic and benthic in habit, an internal exchange of biomass is indicated by the couplings between Phytoplankton and Benthic Algae. Imports of biomass from outside the spatial area of interest to the four functional groups are indicated by an arrow from outside the process to the central node.

Detrital Decomposition

Organic inputs to the process of Detrital Decomposition include the detrital outputs from other biological processes and imports of detritus from outside the spatial area of interest (Figure 6.7). Such inputs are not generated by Detrital Decomposition, and consequently they are represented by arrows between the various sources and Detritus, the only state variable of Detrital Decomposition. It should be noted that the arrow from Consumption to Detritus represents Consumption-generated fecal matter moving into the detritus pool, while the arrow from Consumers represents the simple transfer of dead organisms to Detritus. Detritus includes all dead particulate organic matter and the associated heterotrophic microflora and microfauna. Decomposition of this particulate material stimulates the uptake of inorganic nutrients by the microflora, a process-generated input that is represented by a coupling extending from external nutrient resources to the process (Figure 6.7). The process of Consumption also mechanically reduces detrital particle size, thereby accelerating decomposition by increasing the ratio of particle surface area to volume. Mechanical size reduction does not involve the transfer of material between Consumption and Detrital Decomposition; hence, the effect is indicated by the dashed-line arrow from Consumption to Detrital Decomposition. Process-generated outputs from Detrital Decomposition include respiratory losses by the associated microflora and microfauna and losses of dissolved organic matter. Ingestion of organic matter by detritivores is represented by the arrow extending from Detritus to Consumption.

6.3.3 Consumption

The process of Consumption (Figure 6.8) includes all activities related to the ingestion of the primary food resources by consumers. In this case, the consumers are all heterotrophic organisms excluding bacteria, fungi, and animals that are too small to physically separate from detrital particles without the aid of a microscope. Consumption couples directly with Primary Food Processes (Figure 6.2), and the resource for Consumption is the Primary Food Supply. Inputs of this resource are process-generated, and therefore, are designated by an arrow from the corresponding external state variable to the perimeter of the process circle (Figure 6.8). Process-generated outputs from Consumption are respiratory losses, dissolved organic compounds, and particulate organic matter derived from fecal deposition. The loss of particulate fecal matter is illustrated by the arrow from the process circle to the Primary Food Supply, which includes detritus as part of its biomass. The state variable associated with Consumption at this level of resolution is the biomass of consumer organisms. The transfer of dead organisms from this state variable to the Primary Food Supply, an output that is not generated directly by the process, is indicated by an arrow between the corresponding rectangles. Exports and Imports are indicated according to the convention presented in Figures 6.1 and 6.5.

6.3.4 Subsystems of Consumption

The subsystems of Consumption that are relevant to the CREDDP synthesis include Deposit Feeding, Suspension Feeding, Wetland Herbivory, and Predation (Figure 6.2). Internal couplings are primarily concerned with the consumption of biomass associated with Deposit Feeding, Suspension Feeding, and Wetland Herbivory by the process of Predation. The couplings between Deposit Feeding and Suspension Feeding represent exchanges of biomass that are related to life history phenomena. CREDDP investigations contributing data related to the Consumption subsystem are described in reports by Jones and Bottom (1984), Holton et al. (1984), Simenstad (1984), McConnell et al. (1984), Bottom et al. (1984), Hazel et al. (1984), Dunn et al. (1984), and Jeffries et al. (1984).

Deposit Feeding

Deposit feeders are partitioned into two state variables: Infauna and Epifauna (Figure 6.9). Couplings between Zooplankton, a state variable external to Deposit Feeding, and Infauna and Epifauna represent exchanges of biomass that result from changes in life history stages. For example, certain infauna and epifauna have early developmental stages that are zooplanktonic. Resources for Deposit Feeding include the benthic algae and detritus that are ingested with sediment by epibenthic and infaunal consumer organisms. Process-related outputs from Deposit Feeding are respiratory losses, dissolved organic matter, and fecal material. The latter is transferred to Detritus, an external state variable associated with the Detrital Decomposition subsystem. Losses of infaunal and epifaunal biomass to Predation and export, and the introduction of biomass from outside the spatial area of interest (Import) are represented in the conventional way by arrows connected to the internal state variables.

Suspension Feeding

State variables associated with the process of Suspension Feeding are Infauna, Epifauna and Zooplankton (Figure 6.10). Infaunal and epifaunal suspension feeders exchange biomass with Zooplankton, internal transfers that relate both to life history events and consumption. Figure 6.10 also depicts the same life history-related biomass exchange between deposit feeders and Zooplankton as illustrated in Figure 6.9, except that in Figure 6.10 Zooplankton is illustrated as the internal state variable. Resources for Suspension Feeding include phytoplankton and detritus, whereas all other variables and relationships for the process are the same as those indicated for Deposit Feeding (Figures 6.9 and 6.10).

Wetland Herbivory

The process of Wetland Herbivory has three state variables: Herbivorous Birds, Herbivorous Mammals, and Herbivorous Insects (Figure 6.11). Birds and mammals were investigated by Hazel et al. (1984) and Dunn et al. (1984). Unfortunately the dynamics of insect populations were not investigated by CREDDP researchers. Process-generated resources for Wetland Herbivory are vascular plants from estuarine marshlands and detritus generated by these plants. Process-generated outputs from the system include respiratory losses, losses of dissolved organic matter, and fecal discharge which is transferred to Detritus. Gains and losses acting directly on the state variables are imports and exports of biomass into and out of the spatial area of interest, losses to the process of Predation, and dead herbivores which are transferred to Detritus.

Predation

Predation is a process concerned with the secondary and tertiary consumption of living organisms. State variables associated with Predation include Predatory Invertebrates, Predatory Fish, Predatory Birds, and Predatory Mammals (Figure 6.12). Process-generated resources for Predation are the primary consumer organisms, namely zooplankton, many infaunal and epifaunal organisms, and the herbivorous birds, mammals, and insects. In addition, predators can eat each other, and these transfers of organic matter are indicated by the couplings between the internal state variables. Predation also contributes to the detrital biomass by transfer of fecal material and the remains of dead organisms. The former is process-generated, while the latter is simply a change in state, i.e., from living to dead organic matter. Imports, exports, and process-generated losses of respiratory products and dissolved organic matter are represented as in Figures 6.5-6.11.

6.4 SUMMARY

The process model presented in the sections of this chapter provides the conceptual structure for the organization of the biological information presented in Chapters 7 and 8. In Chapter 7, emphasis is placed on the dynamics of the biological processes represented in Figure 6.2 and Figures 6.5-6.12 and on the CREDDP information corresponding to the inputs, outputs, and coupling variables associated with each process. Therefore, Chapter 7 is primarily concerned with biological and physical mechanisms that account for the functional and structural attributes of the biological components of the Columbia River Estuary. In Chapter 7, model structure also is used to identify deficiencies in the CREDDP data base, a function that can help establish priorities for future research. Chapter 8 is a descriptive, regional summary of CREDDP biological data which is based on the process model (Figures 6.2 and 6.5-6.12) and on the spatial conceptualization of the estuary (Figure 6.4). In Chapter 8, the taxa associated with each biological process are listed by region and habitat type, and the production and mean biomass related to each process for the habitat types in each region are summarized on an annual time resolution.

PRIMARY FOOD PROCESSES

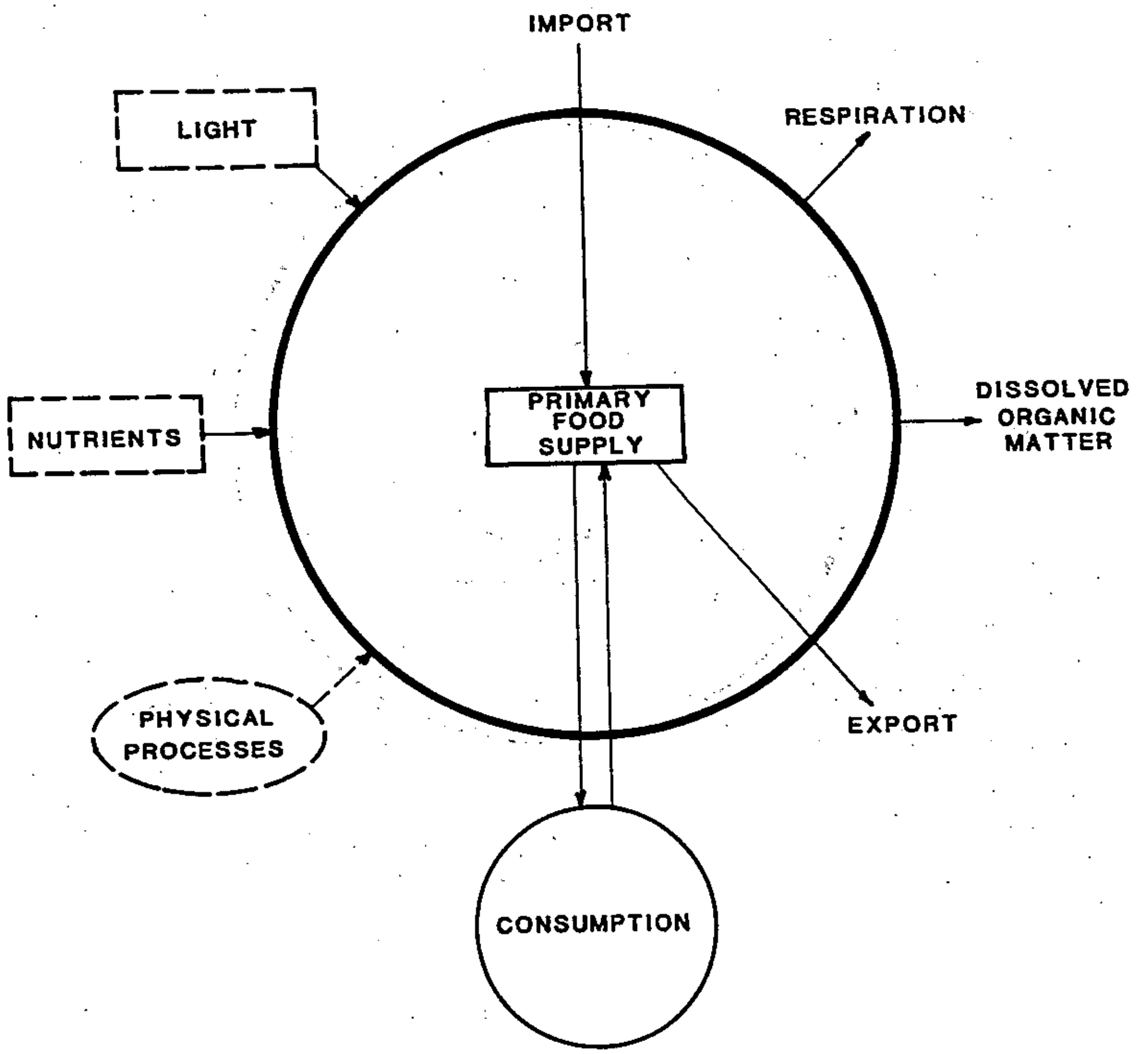


Figure 6.5. A diagram of Primary Food Processes, a subsystem of Estuarine Biological Processes.

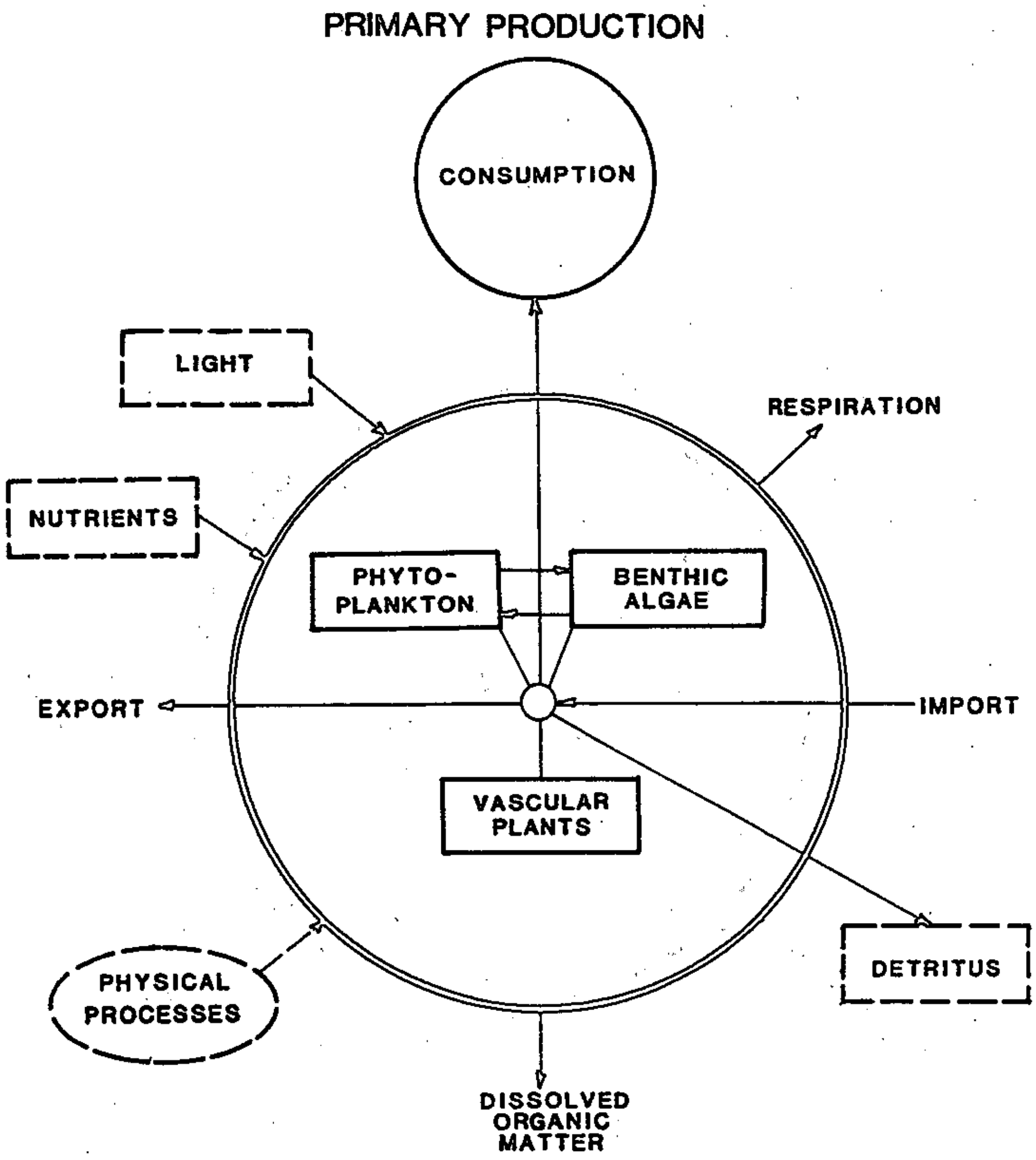


Figure 6.6. Primary Production, a subsystem of Primary Food Processes. Central node indicates relationships common to all state variables.

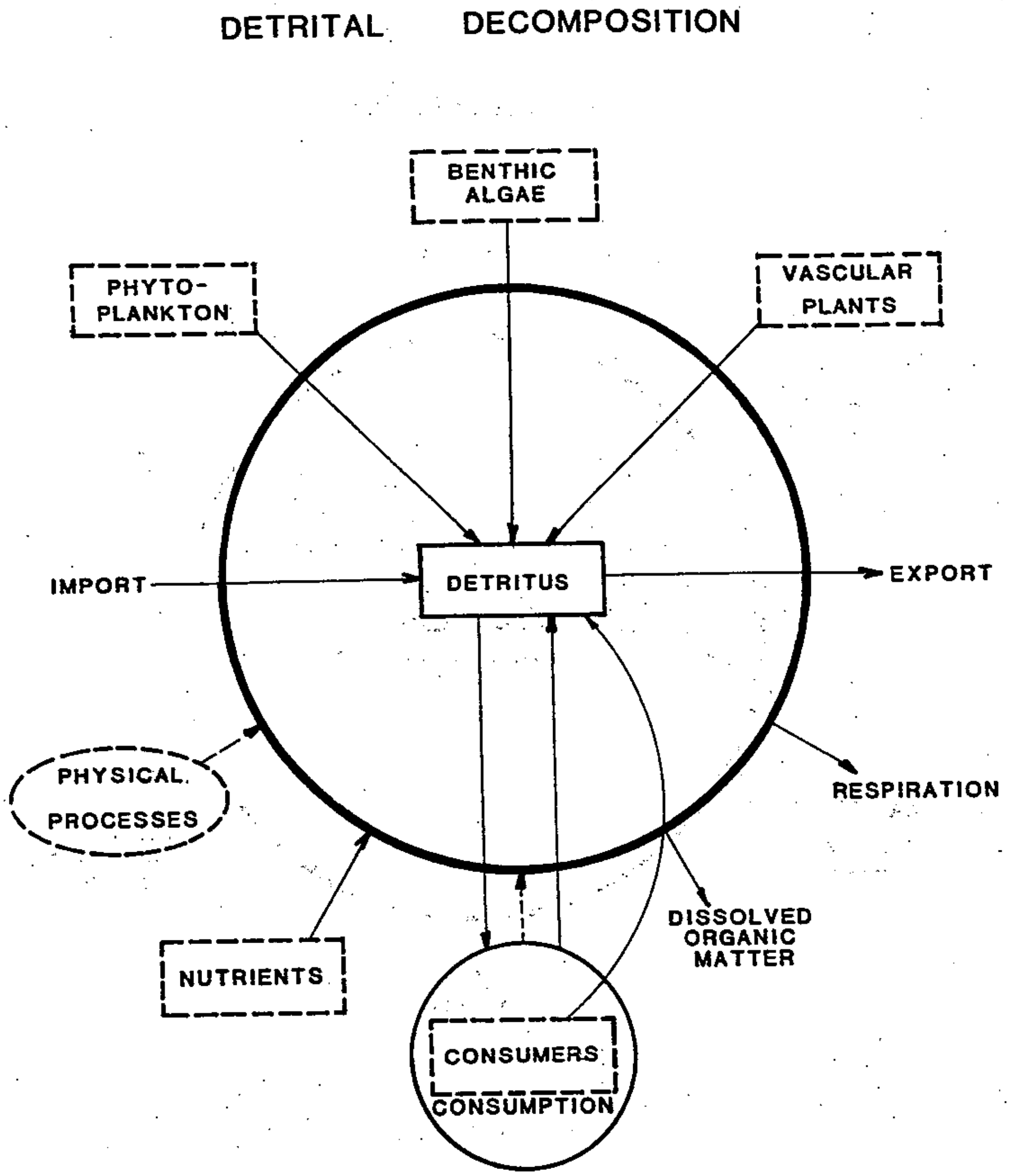


Figure 6.7. Detrital Decomposition, a subsystem of Primary Food Processes.

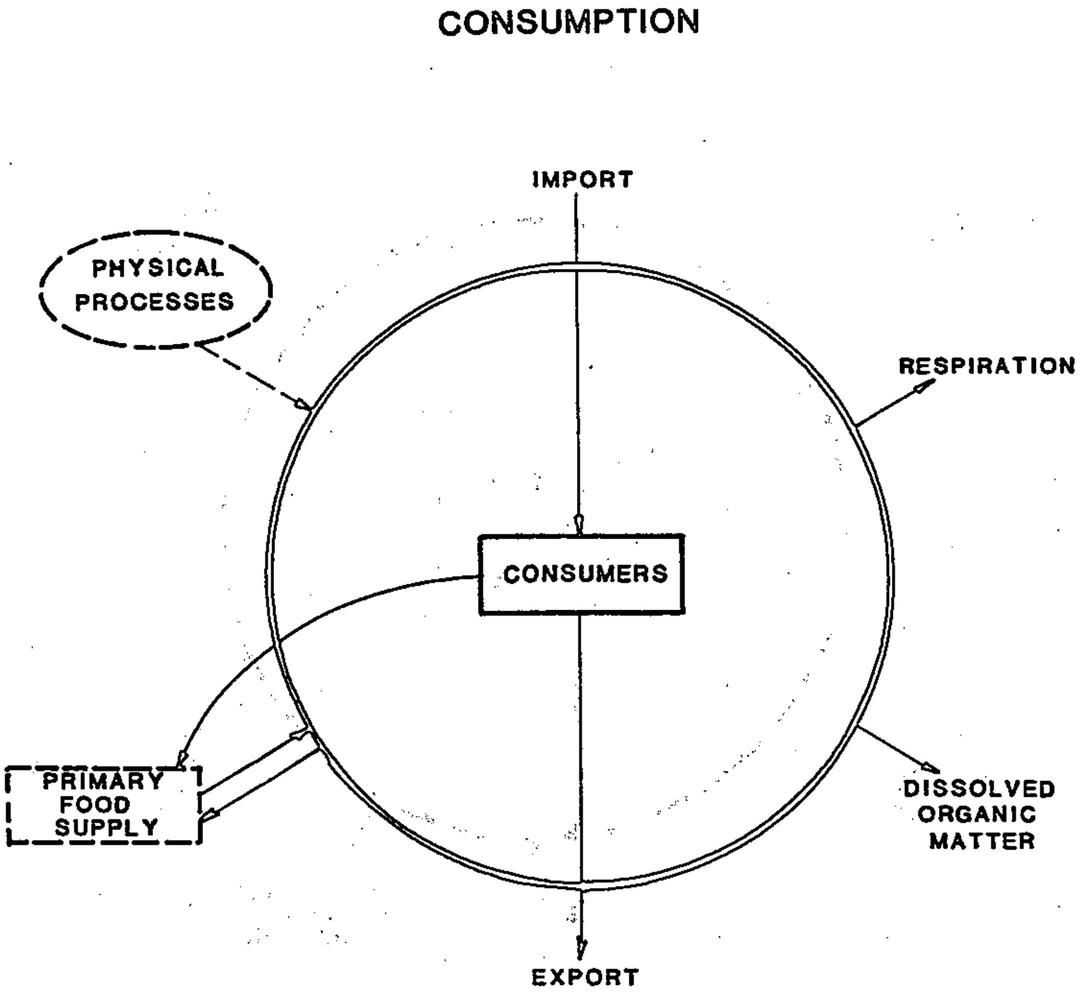


Figure 6.8. Consumption, a subsystem of Estuarine Biological Processes.

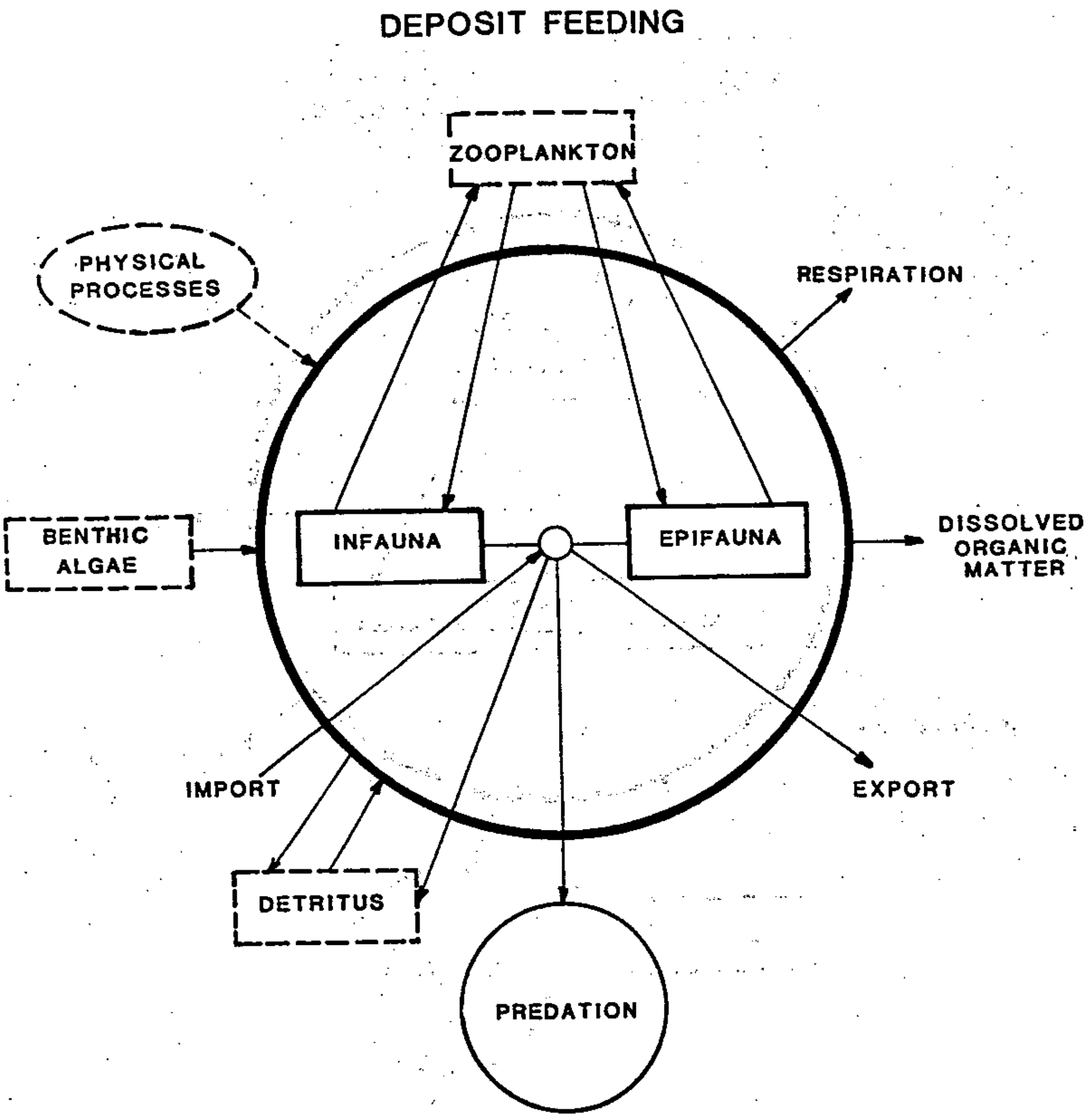


Figure 6.9. Deposit Feeding, a subsystem of Consumption.

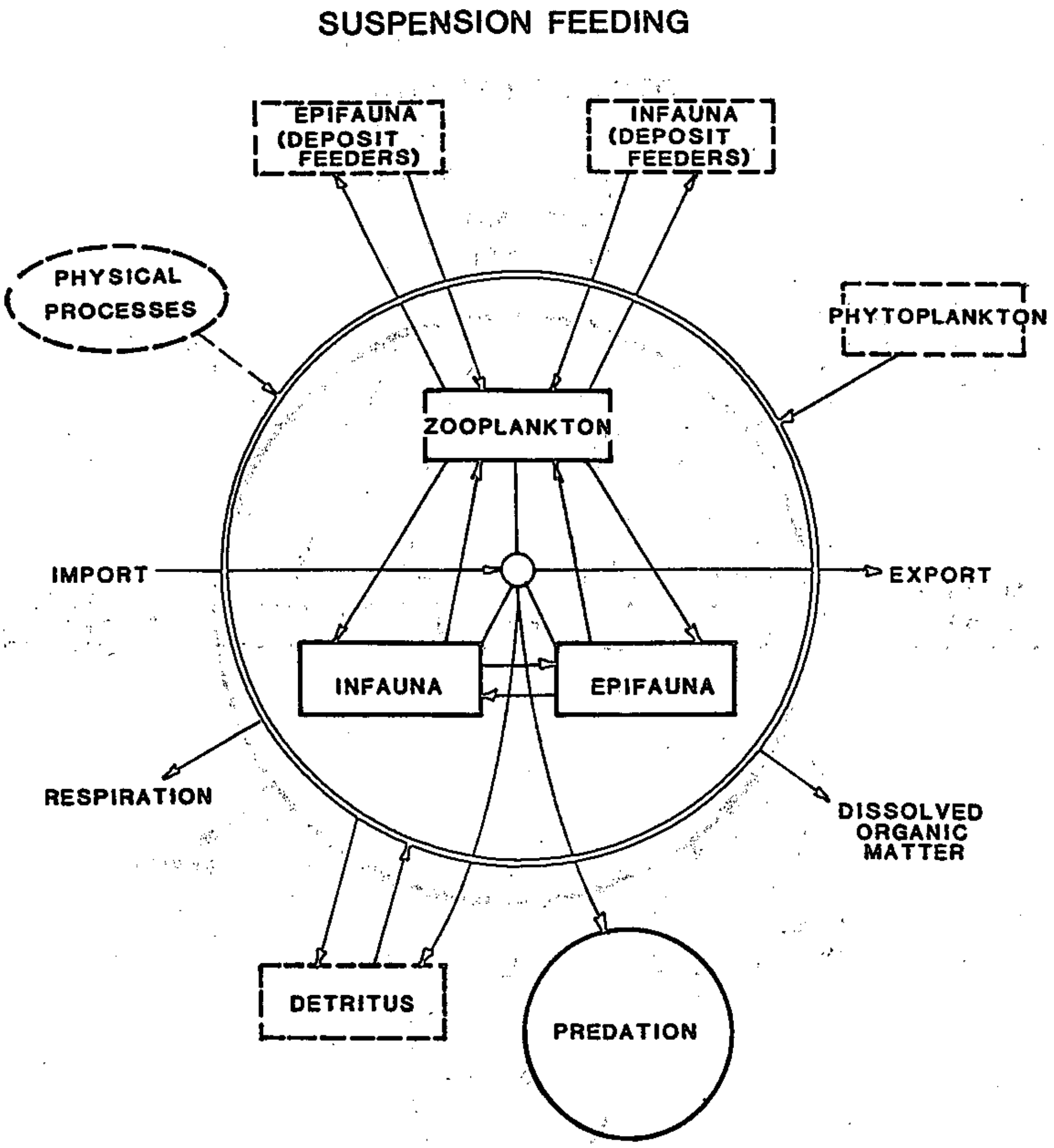


Figure 6.10. Suspension Feeding, a subsystem of Consumption.

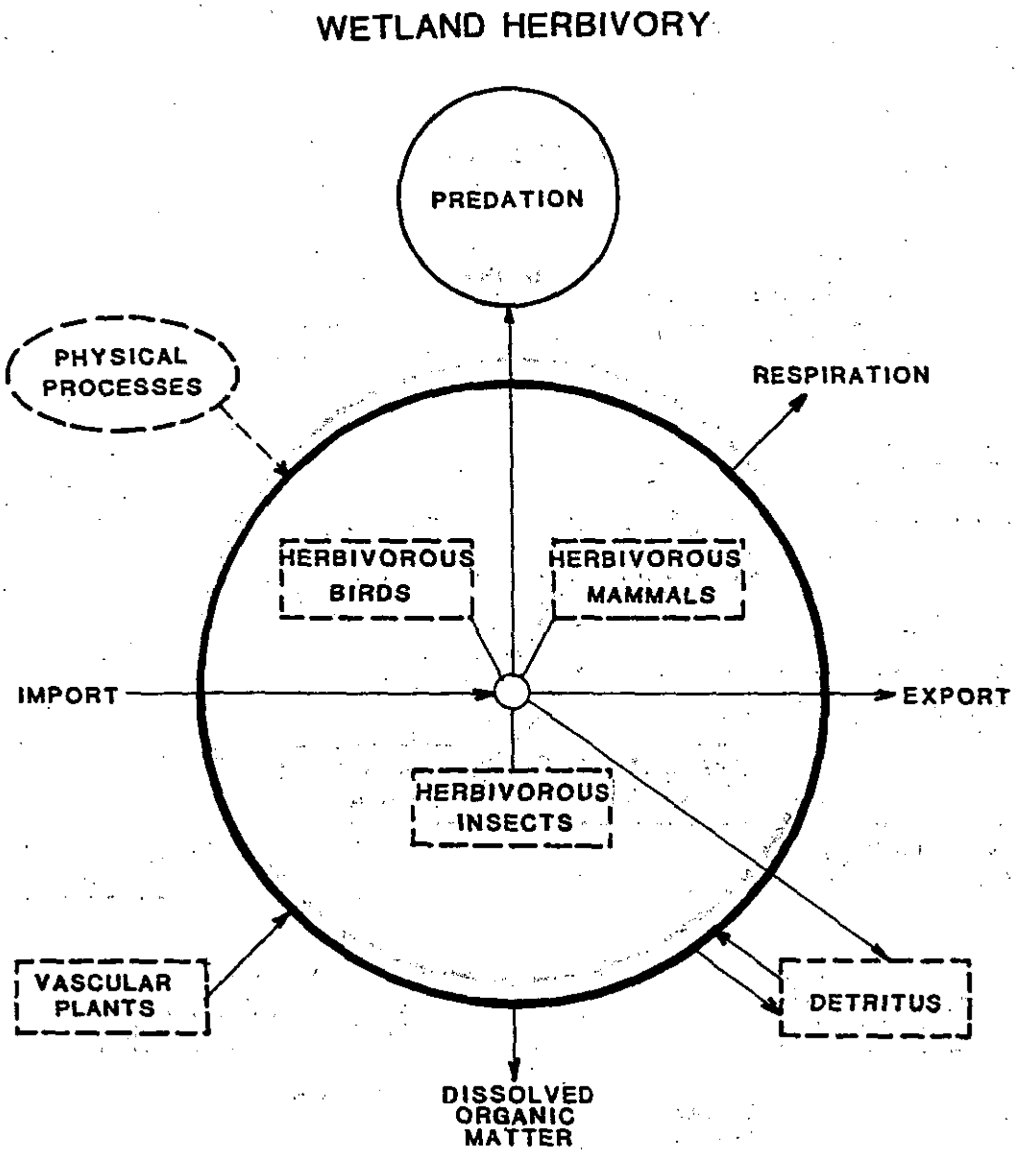


Figure 6.11. Wetland Herbivory, a subsystem of Consumption.

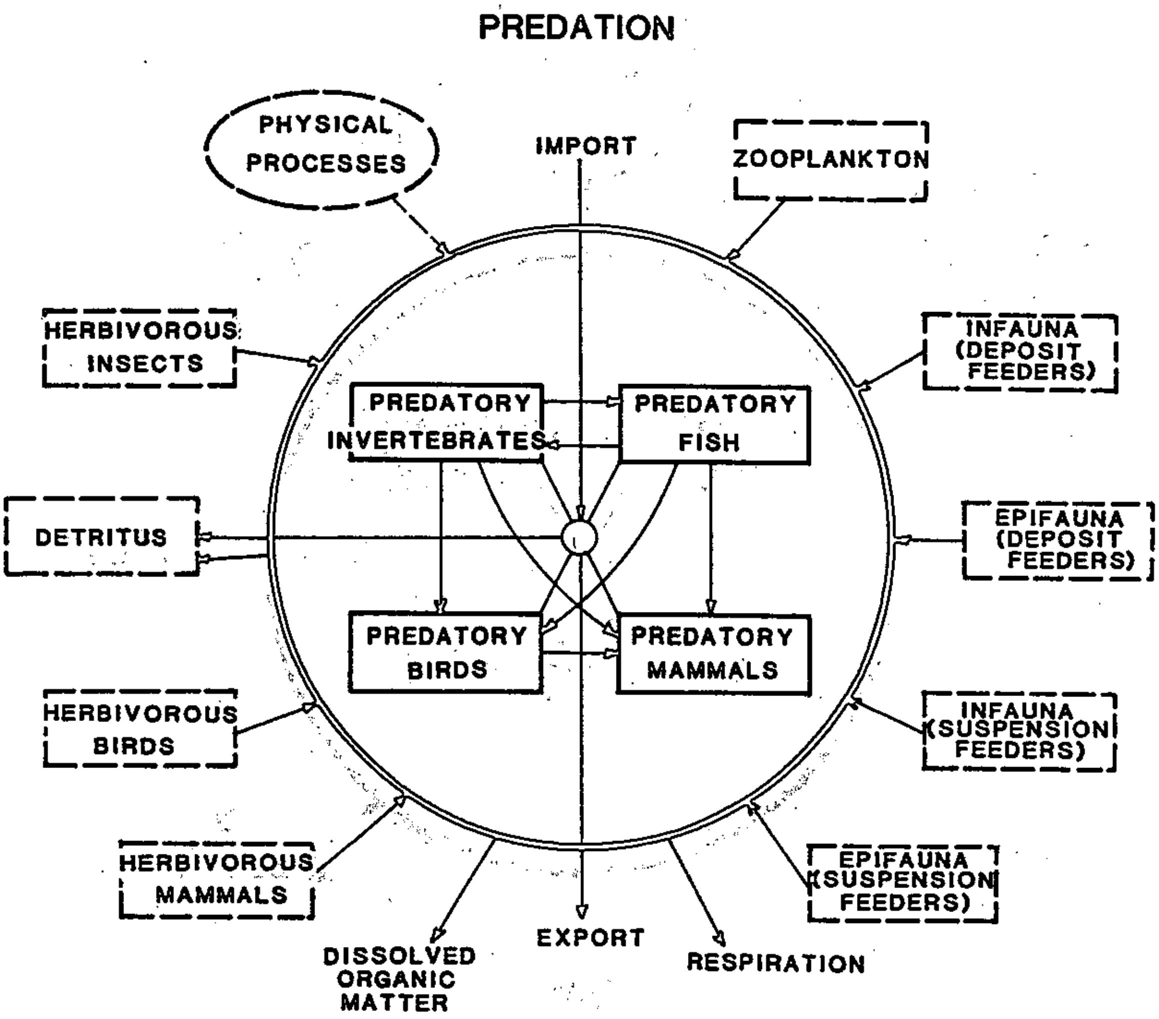


Figure 6.12. Predation, a subsystem of Consumption.

7. ECOSYSTEM PROCESSES

This chapter is concerned with the patterns and mechanisms associated with the dynamics of biological processes in the Columbia River Estuary. The organization of the chapter is based on the processes introduced in Chapter 6. In Sections 7.1 and 7.2 the subsystems of Primary Food Processes are discussed, while the dynamics of the subsystems of Consumption are reported in Section 7.3. In each of these sections the discussion corresponds to the process components introduced in Figure 6.1, i.e., to the state variables, process-generated inputs and outputs, non-process-generated inputs and outputs, and controlling physical variables. In most cases, state variables are expressed in terms of biomasses associated with each process and the taxonomic composition of that biomass.

Some of the discussion of process dynamics requires reference to specific site, area, or regional locations in the Columbia River Estuary. For comparative purposes, the estuary has been divided into three zones and ten regions, a division that is based on river hydrology, circulatory processes, and sedimentary geology (Figure 7.1). The plume and ocean zone corresponds to the Entrance Region, whereas the estuarine mixing zone is partitioned into four regions: Baker Bay plus Trestle Bay, Youngs Bay, the Estuarine Channels Region, and the Mid-Estuary Shoals Region. The tidal fluvial zone is divided into Grays Bay, Cathlamet Bay, and the Fluvial Region in the upper estuary. In addition, the Youngs River and Lewis and Clark River, both tributaries into Youngs Bay, are designated as a separate region in this chapter; and Deep River, a tributary of Grays Bay, also is considered as a separate region.

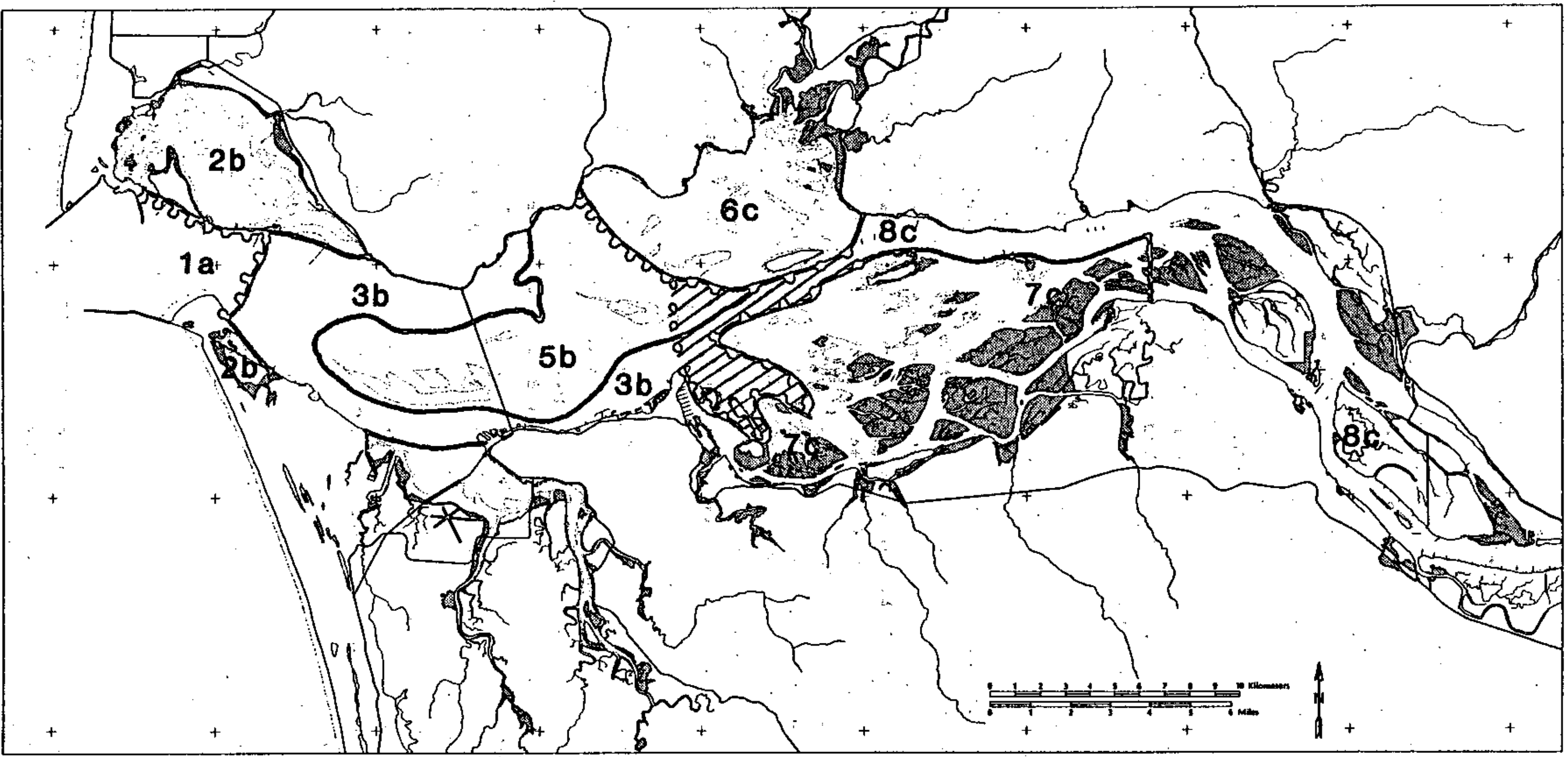
Investigators also have defined six habitat types which are compatible with the distributional patterns of various functional groups of estuarine organisms. The major habitat types under consideration are high marsh and swamp, low marsh, tidal shoals and flats, demersal slope, channel bottom, and water column. The water column habitat type occurs in all ten regions of the estuary, while the other five habitat types may or may not be present in a particular region, depending on the regional location relative to the ocean and shoreline. A detailed description of the zones, regions, and habitat types, along with a corresponding summary of annual production and taxonomic composition, is presented in Chapter 8.

7.1. PRIMARY FOOD PROCESSES: PRIMARY PRODUCTION

7.1.1 Introduction

Model and Couplings

The state variables of the Primary Production subsystem are the biomasses of phytoplankton, benthic algae, and vascular hydrophytes (Figure 7.2). Light and nutrients drive in primary production through



Regions

1 - Entrance
2 - Baker Bay and Trestle Bay
3 - Estuarine Channels
4 - Youngs Bay
5 - Mid-estuary Shoals
6 - Grays Bay
7 - Cathlamet Bay
8 - Fluvial Region
9 - Youngs and Lewis & Clark Rivers
10 - Deep River

Zones

a - Plume and Ocean
b - Estuarine Mixing
c - Tidal Fluvial

Shaded area is in the tidal fluvial zone, except during the low riverflow season, when it is part of the estuarine mixing zone.

Figure 7.1. Estuarine regions delineated by the Columbia River Estuary Data Development Program.

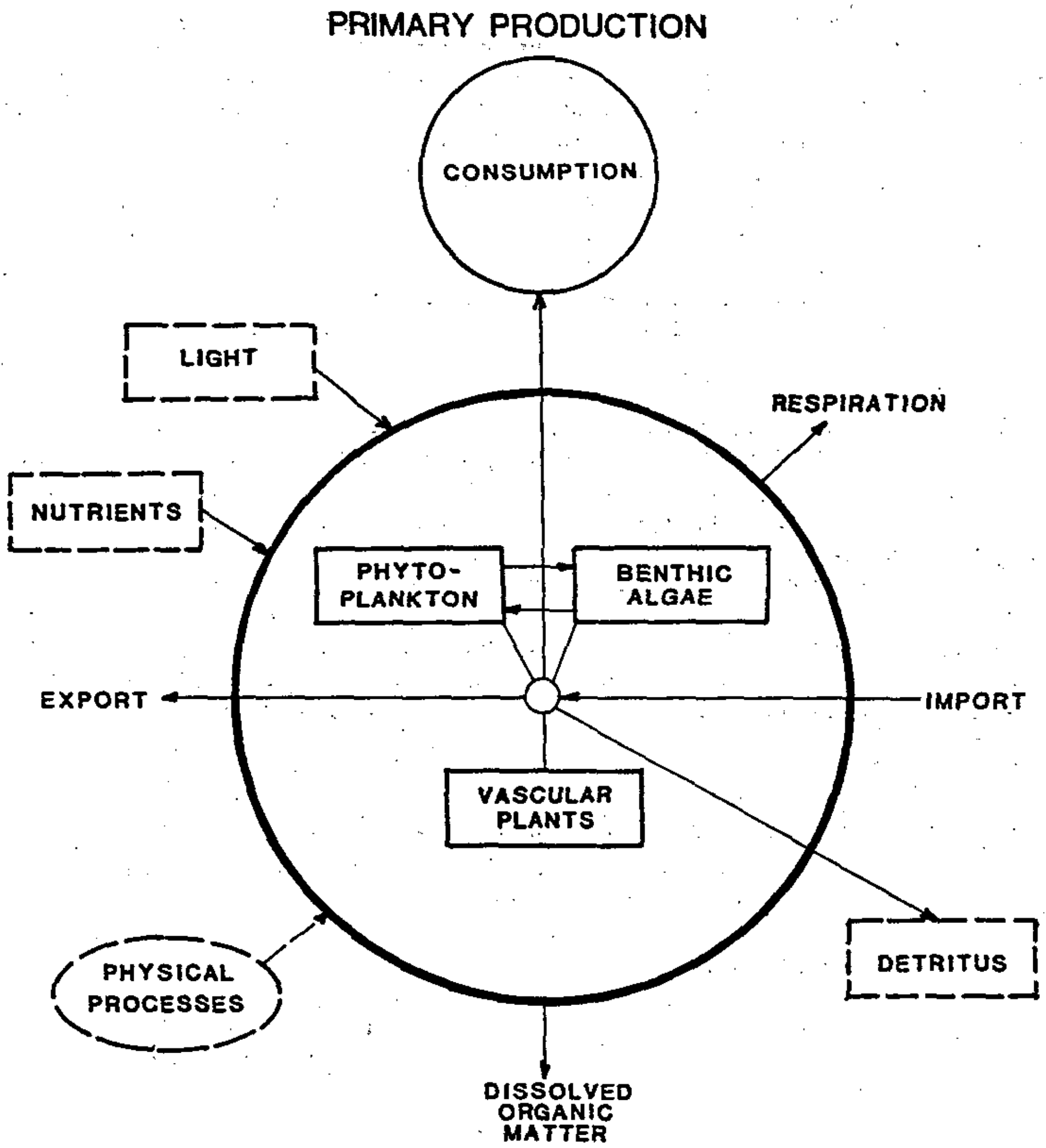


Figure 7.2. Primary Production, a subsystem of Primary Food Processes. Central node indicates relationships common to all state variables.

the biochemical process of photosynthesis and through nutrient uptake and assimilation. Respiration and excretion of dissolved substances from plant cells represent process-generated losses. The net difference between autotrophic production and concurrent respiratory and excretory losses is equivalent to net primary production when all other processes of biomass removal (e.g., consumption and export) are not considered. Physical variables controlling or affecting primary production, in addition to light energy and nutrient supply, can include water temperature, salinity, freshwater interfaces and the tidal cycle. Biomass losses from the three state variables occur in three ways: 1) export of living plant material out of the estuary or any selected section of the estuary; 2) transfer of dead plants to the detrital pool; and 3) removal of live plant material through various consumption processes. Living plant biomass, particularly phytoplankton, also can be imported to the estuary from the river or ocean. Importation, by definition, does not involve photosynthetically generated increases in plant biomass within the spatial area under consideration. Nominally, benthic microalgal species are considered as phytoplankton when they are found in the water column as a result of turbulence or other means. Similarly, phytoplankton cells that settle out on some substrate and continue metabolizing are treated as benthic microalgae. The two arrows between Phytoplankton and Benthic Algae in Figure 7.2 represent this exchange of cells between the water column and the benthos.

Data Base

The data base for the phytoplankton portion of the Primary Production subsystem derives from nine cruises on the Columbia River Estuary, sequenced approximately every other month from April 1980 to July 1981. Station locations included shallow areas and most bays as well as the main channel (Figure 7.3). Except in June and July 1981, when only three stations were sampled for specialized studies, the number of stations sampled per cruise varied from 25 to 47. All stations were sampled at the water surface, and at selected stations samples were collected at depths of 2.5, 5.0, and 10 meters.

Details of assessment of spatial and temporal variability of detrital particles and of living phytoplankton biomass and/or productivity are given by Frey et al. (1984). Measurements included concentrations of chlorophyll a and phaeophytin a, *in vivo* fluorescence with and without DCMU treatment, concentrations of total suspended particles, the organic and inorganic fractions of total suspended load, concentrations of particulate carbon and nitrogen, and carbon-14 productivity. Incoming and penetrating light, and concentrations of dissolved inorganic nutrients (nitrate plus nitrite, phosphate and silicate), were measured as resource inputs. Several special studies were made to assess grazing removal of suspended particles by zooplankton. Temperature was measured as a physical variable with potential to affect phytoplankton metabolism and distribution. Salinity and current velocity data were supplied by other groups to aid in the interpretation of the distribution and abundance of phytoplankton. In addition to the work of Frey et al. (1984), Lara-Lara (1983) has discussed some of the data, and effects of the eruption of Mount St. Helens on primary productivity have been reported by Frey et al. (in press).

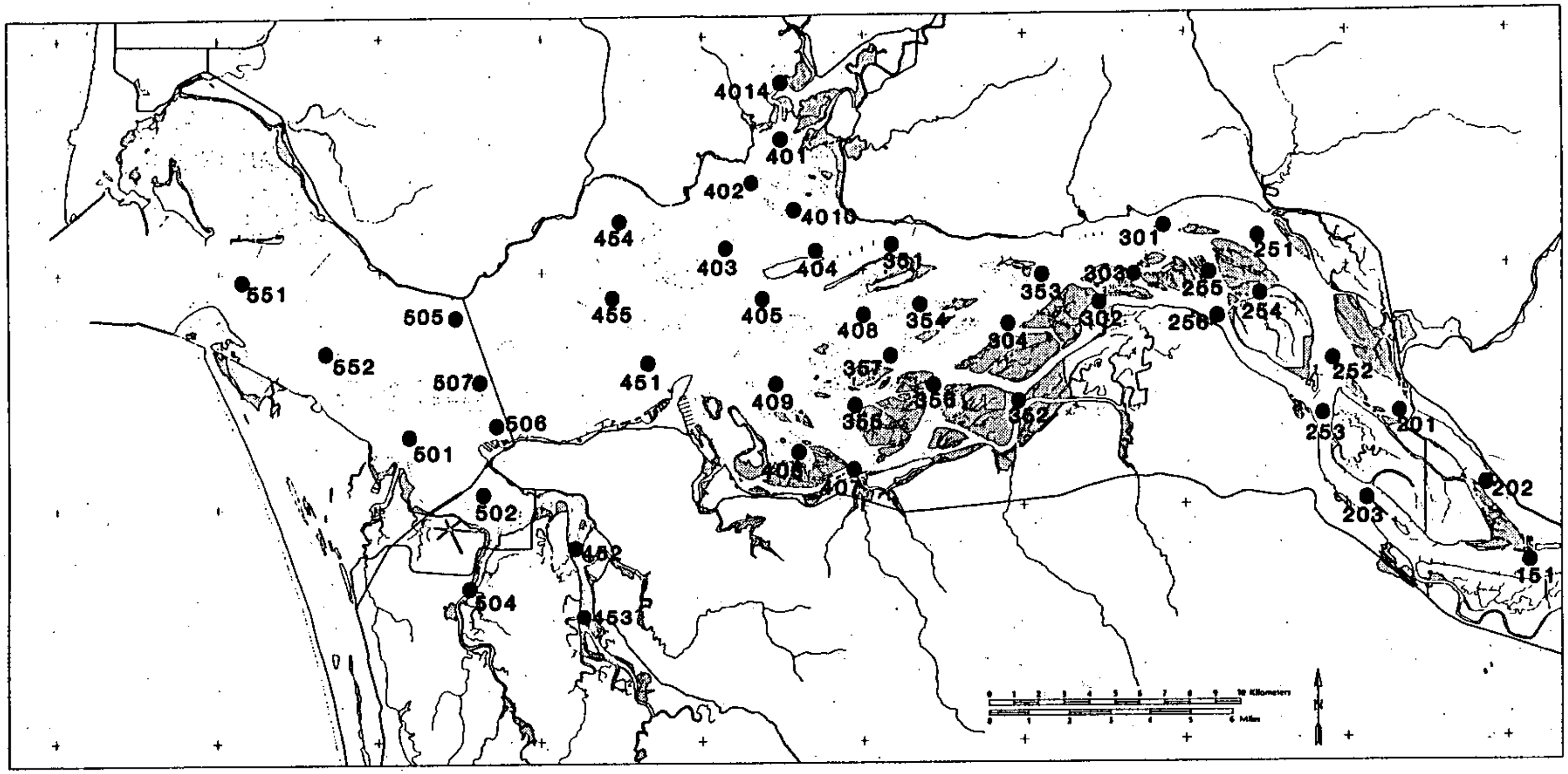


Figure 7.3. Sampling stations for the investigation of water-column primary production in the Columbia River Estuary.

Seaweeds and other macroalgae are relatively insignificant in the Columbia River Estuary as a whole, and therefore have not been considered in any quantitative way in this study. The data base related to the functional and structural attributes of benthic algal assemblages refers to microalgal assemblages. This data base was generated from monthly, replicated sampling at five intensive study sites in the estuary, and from a broad survey involving the collection of samples from 31 other sites (Figure 7.4). The investigation at the intensive study sites continued from April 1980 through April 1981, while sampling at the survey sites occurred during the period from early May 1981 through the month of August 1981. The sampling strategy at each intensive study site involved the collection of sediment cores for the analysis of chlorophyll a and phaeo-pigment concentrations and for measurements of primary productivity in a respirometer chamber. Other variables monitored at the intensive study sites included salinity, temperature, community oxygen uptake, and the concentration of organic matter in the top centimeter of sediment. In addition, sediment samples were obtained for a distributional analysis of grain size. Samples were collected along 25-m transects in the lower, mid and upper intertidal regions of the intensive study sites, and in the lower marsh below the emergent plant vegetation. At the survey sites, chlorophyll a and phaeo-pigment concentrations in the sediment also were measured along transects in the lower, mid and upper intertidal regions. Ten of the survey sites were selected to validate predictions of primary productivity which were based on relationships established during the investigation at the intensive study sites. Regression equations derived from data collected from the intensive study sites were used to predict rates of primary production from measurements of sediment chlorophyll at the validation sites, and the predicted values were checked against field measurements of primary productivity at the validation sites.

In August 1982, a taxonomic study of the diatom flora of the Columbia River Estuary was undertaken. This study involved the examination of 56 samples, 49 of which were obtained from benthic habitats and 7 of which were plankton samples from the water column. Over 17,000 diatom valves were identified and counted, approximately 300 per sample.

The data base related to the functional and structural attributes of vascular plants in the Columbia River Estuary was derived from 22 locations at 15 intensive study sites (Figure 7.5). Species abundance at each site was expressed in terms of percentage cover. All sites but the Typha marsh on Puget Island were sampled twice during the study, once in July 1980 and again in August 1981. Thus, the data matrix for the species abundance work represented 43 samples, with 49 species being identified. In addition to these data, Thomas (1983) recently surveyed the region corresponding to the first 40 river miles, and identified 165 species of vascular plants, 11 of which were associated with tidal flats and subtidal areas.

Biomass of above-ground vegetation, both live and attached standing dead biomass from the same season's growth, was determined from 0.1 m^2 quadrats at each of the 15 intensive study sites (Figure 7.5). Quadrats

Seaweeds and other macroalgae are relatively insignificant in the Columbia River Estuary as a whole, and therefore have not been considered in any quantitative way in this study. The data base related to the functional and structural attributes of benthic algal assemblages refers to microalgal assemblages. This data base was generated from monthly, replicated sampling at five intensive study sites in the estuary, and from a broad survey involving the collection of samples from 31 other sites (Figure 7.4). The investigation at the intensive study sites continued from April 1980 through April 1981, while sampling at the survey sites occurred during the period from early May 1981 through the month of August 1981. The sampling strategy at each intensive study site involved the collection of sediment cores for the analysis of chlorophyll a and phaeo-pigment concentrations and for measurements of primary productivity in a respirometer chamber. Other variables monitored at the intensive study sites included salinity, temperature, community oxygen uptake, and the concentration of organic matter in the top centimeter of sediment. In addition, sediment samples were obtained for a distributional analysis of grain size. Samples were collected along 25-m transects in the lower, mid and upper intertidal regions of the intensive study sites, and in the lower marsh below the emergent plant vegetation. At the survey sites, chlorophyll a and phaeo-pigment concentrations in the sediment also were measured along transects in the lower, mid and upper intertidal regions. Ten of the survey sites were selected to validate predictions of primary productivity which were based on relationships established during the investigation at the intensive study sites. Regression equations derived from data collected from the intensive study sites were used to predict rates of primary production from measurements of sediment chlorophyll at the validation sites, and the predicted values were checked against field measurements of primary productivity at the validation sites.

In August 1982, a taxonomic study of the diatom flora of the Columbia River Estuary was undertaken. This study involved the examination of 56 samples, 49 of which were obtained from benthic habitats and 7 of which were plankton samples from the water column. Over 17,000 diatom valves were identified and counted, approximately 300 per sample.

The data base related to the functional and structural attributes of vascular plants in the Columbia River Estuary was derived from 22 locations at 15 intensive study sites (Figure 7.5). Species abundance at each site was expressed in terms of percentage cover. All sites but the Typha marsh on Puget Island were sampled twice during the study, once in July 1980 and again in August 1981. Thus, the data matrix for the species abundance work represented 43 samples, with 49 species being identified. In addition to these data, Thomas (1983) recently surveyed the region corresponding to the first 40 river miles, and identified 165 species of vascular plants, 11 of which were associated with tidal flats and subtidal areas.

Biomass of above-ground vegetation, both live and attached standing dead biomass from the same season's growth, was determined from 0.1 m^2 quadrats at each of the 15 intensive study sites (Figure 7.5). Quadrats

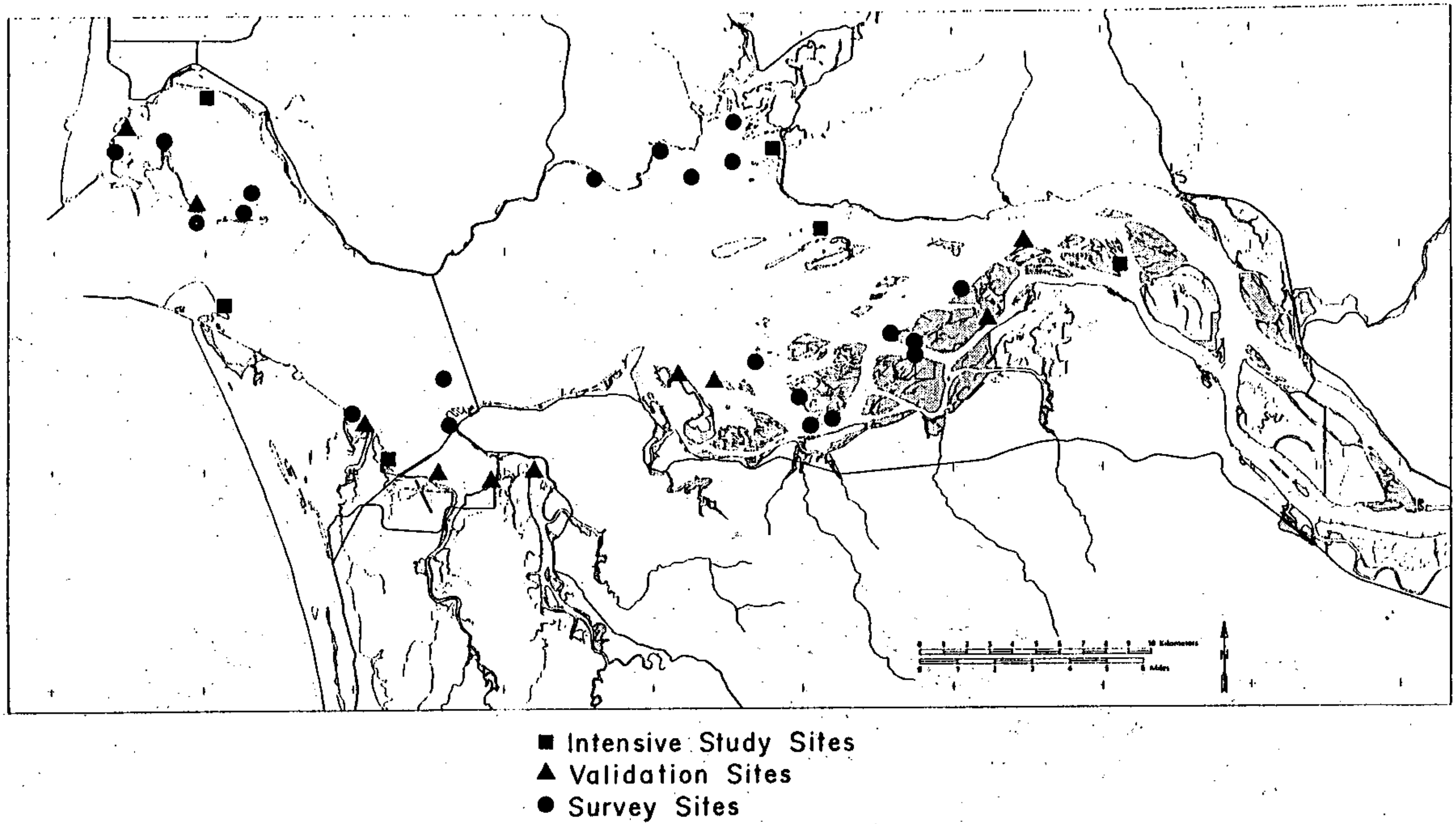


Figure 7.4. Sampling sites for the investigation of benthic primary production in the Columbia River Estuary.

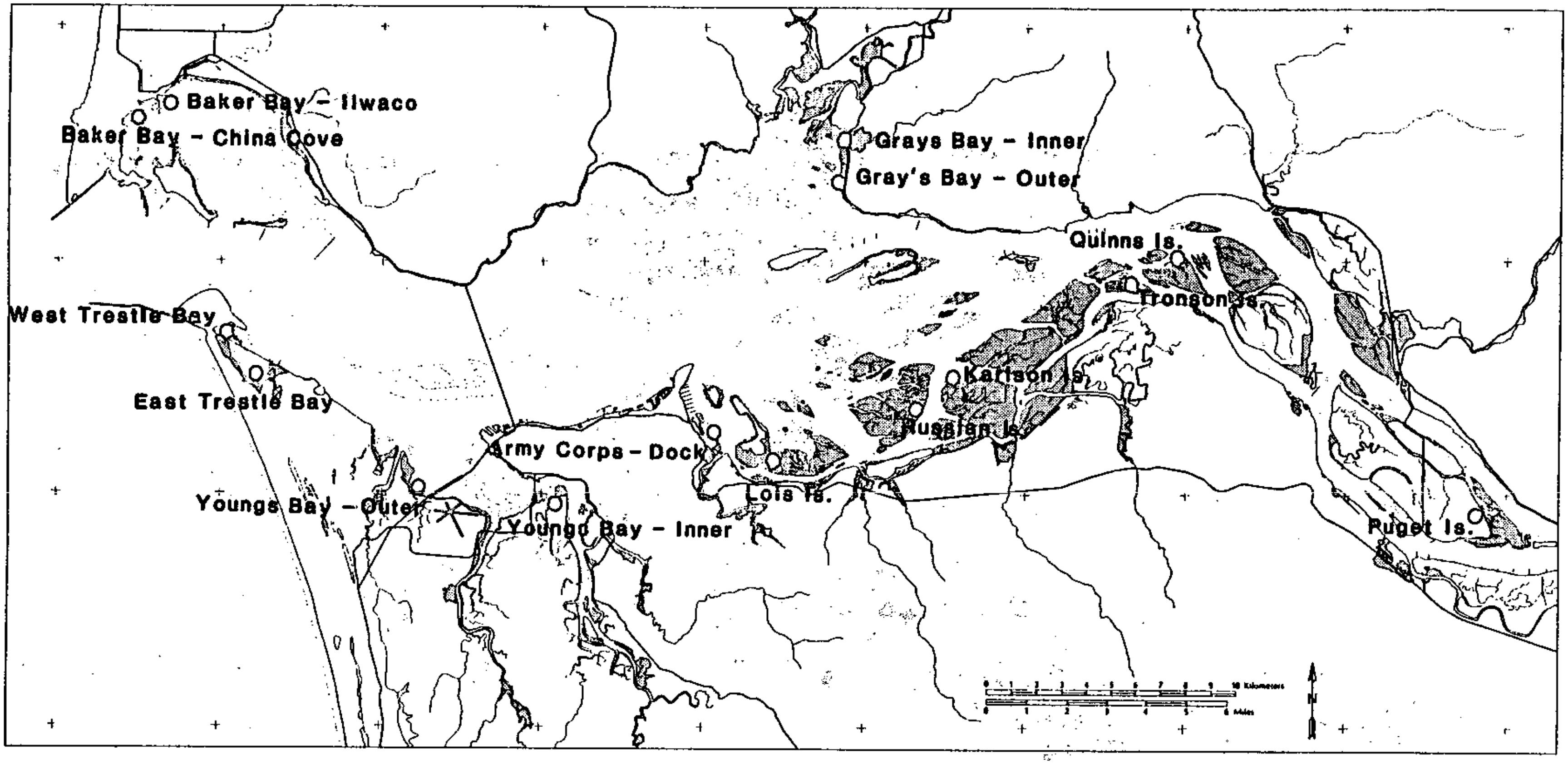


Figure 7.5. Sampling sites for the investigation of emergent plants in the Columbia River Estuary.

were taken from visibly uniform stands in both high and low marsh areas, when such areas were present at a study site. At some locations, below-ground material (roots and rhizomes) was taken in 8 cm diameter x 20 cm long cores. Annual marsh plant production was estimated from the maximum biomass values at each site.

7.1.2 Taxonomic Structure of Plant Assemblages

The conceptual model of the Primary Production subsystem represents the plants of the Columbia River Estuary as three functional groups: phytoplankton, benthic algae, and vascular plants. The biomasses of these groups are the internal state variables in the systems diagram presented in Figure 7.2. Although the process of primary production is continuous in aquatic ecosystems with adequate light energy and nutrients, changes in the species composition (i.e., in the genetic information involved in the primary production process) may change the productive capacities of the systems as environmental conditions fluctuate in time and space. In addition, a description of the taxonomic structure of plant communities aids in habitat classification and in the identification of discontinuities in chemical and physical gradients.

Phytoplankton

In the Columbia River Estuary, the phytoplankton greater than 10 um is composed primarily of freshwater diatoms, which represent a downstream extension of the riverine flora. No attempt was made to examine the small microplankton less than 10 um in size. Of the seven plankton samples that were analyzed quantitatively, the October 1980 collection from the channel near Clatsop Spit was the only sample that contained an abundance of marine planktonic diatoms (75.1% of the sample). The typical marine forms included Actinoptychus undulatus, Actinocyclus ehrenbergi, Asteromphalus heptactis, Bacteriastrum delicatulum, Biddulphia longicruris, Chaetoceros decipiens, Chaetoceros radicans, Coscinodiscus perforatus v. cellulosa, Coscinodiscus curvatulus, Ditylum brightwellii, Eucampia zoodiacis, and Skeletonema costatum. A few freshwater planktonic species were also present at low densities (19.4% of the sample), indicating that some mixing with the upriver flora had occurred. The most prominent of these species were Asterionella formosa, Fragilaria crotonensis, Melosira granulata, and Melosira italica. The remainder of the sample contained a mixture of benthic forms that apparently had been dislodged by water movements. A collection of phytoplankton in April 1981 from the channel near Clatsop Spit was dissimilar to the October sample from the same location. The April flora was dominated by typical freshwater taxa, namely Asterionella formosa (45.8%), two unidentified species of Stephanodiscus (12.7% and 11.6%), and Melosira italica (8.1%). The only marine planktonic species in this sample were Chaetoceros decipiens (2.6%) and Skeletonema costatum (1.6%). Relatively few benthic taxa were present in the April sample.

Differences between the October and April water-column samples from the channel near Clatsop Spit were related to seasonal fluctuations in freshwater discharge. Each year a spring freshet increases stratification and reduces salinity intrusion into the estuary (see Chapters 2 and 3). Under these conditions certain freshwater taxa can be found in the upper part of the water column near the mouth of the estuary. In the fall when freshwater discharge is relatively low, stratification is reduced and tidal fluctuations transport the marine phytoplankton further up the estuary.

Plankton samples obtained in October 1980 and April 1981 from the water column near Tongue Point contained mostly freshwater species (98% freshwater planktonic taxa in October, and 90% in April). The slight differences between the October and April samples were attributed to seasonal changes in the relative abundances of the dominant freshwater species. Causes of these seasonal changes were not known specifically, but undoubtedly they were related to seasonal changes in freshwater flow, residence time of water behind upriver dams, and seasonal changes in light, turbidity, nutrient availability (including micronutrients such as trace metals), and possibly temperature.

The phytoplankton sample obtained in the upper estuary near Puget Island in October 1980 consisted of 99% freshwater planktonic taxa and 1% freshwater benthic taxa. The species composition of this sample was similar to that found for the October sample from the water column near Tongue Point.

Small changes in salinity often can bring about large and immediate changes in the species composition of phytoplankton, particularly of freshwater phytoplankton assemblages that encounter saline waters as they are moved downstream. As the salinity intrusion length and stratification shift seasonally and during the tidal month (see Chapter 3), the phytoplankton species composition is affected. For example, in a study in which nine freshwater diatoms were counted in April, July and September 1980 over a small salinity gradient of zero to 5°/oo in the vicinity of Tongue Point, all nine declined markedly in number with increasing salt content of the water (Figure 7.6). All species except *Melosira granulata* disappeared when salinity reached 4°/oo in April. Two species essentially disappeared from samples at 2.5°/oo in July, and six species were either gone or exceedingly rare at a salinity of 5°/oo in September. Of the diatom species examined, *Melosira granulata* and *Asterionella formosa* were most tolerant of salt. These two species are commonly found, though in low numbers, in the channel near Clatsop Spit, as indicated earlier.

In contrast to phytoplankton collections from the lower Columbia River Estuary, planktonic assemblages in the lower Youngs River in November and April consisted of large percentages of freshwater benthic diatoms. A sample obtained in April 1981 was dominated by *Nitzschia palea* (52.8%), *Surirella ovata* (8.5%), *Asterionella formosa* (6.8%), and an unidentified species of *Stephanodiscus* (6.5%). In this case, *N. palea* and *S. ovata* were benthic taxa, while *A. formosa* was planktonic in fresh water. A sample from the same location in November 1981 was dominated by typical freshwater planktonic taxa, namely *Melosira italica* (15.2%), an unidentified species of *Cyclotella* (11.7%), *Asterionella formosa* (9.1%), and an unidentified species of *Stephanodiscus* (8.7%). The November collection contained relatively few living cells, and the

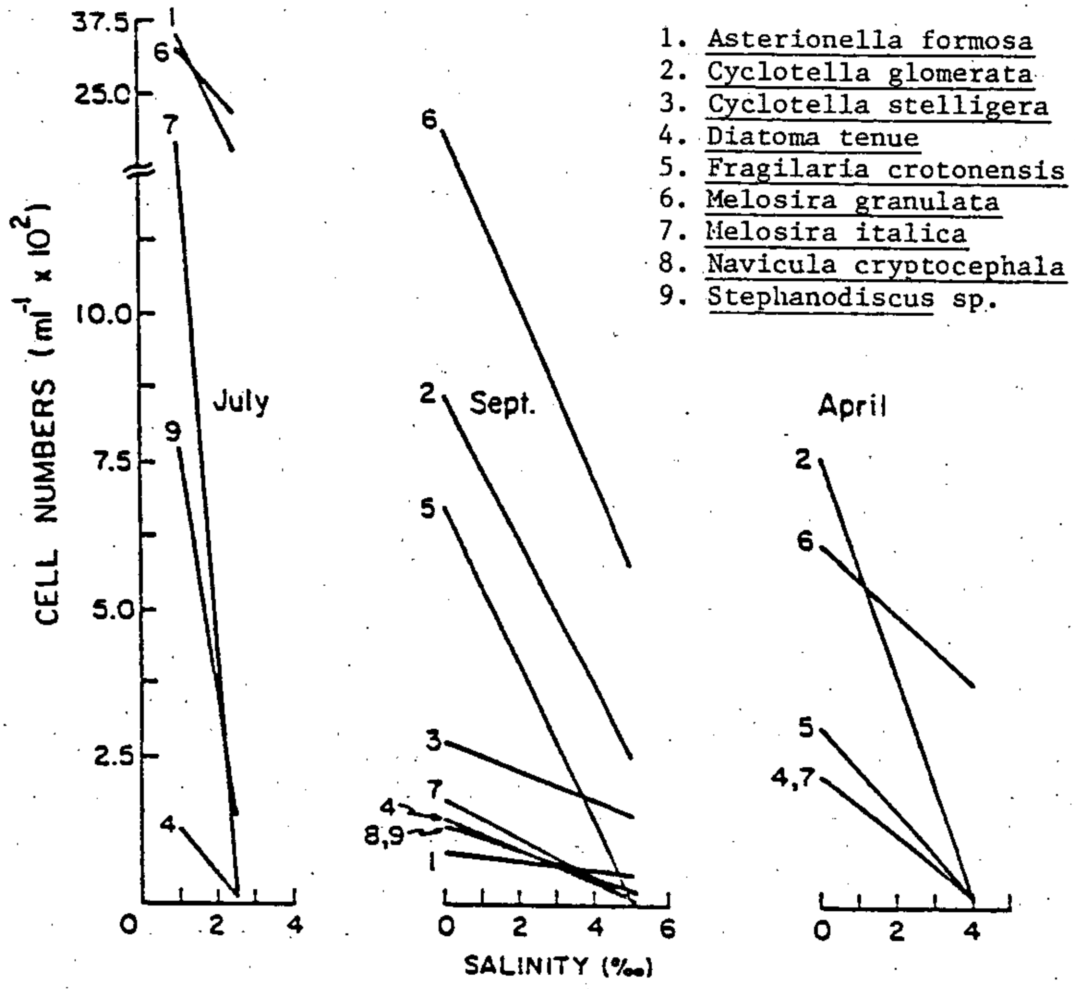


Figure 7.6. Freshwater diatom abundances (cell numbers/ml^{-1} x 100) as a function of salinity from 0 to 5ppt.

presence of marine and brackishwater taxa in this sample (e.g., *Opephora schulzi*, *Campylosira cymbelliformis* and *Chaetoceros subtile*) was evidence of particle transport from the lower estuary and Youngs Bay into the Youngs River. Moreover, the species composition of the samples from the Youngs River indicated that this tributary contributed benthic diatom frustules from freshwater habitats upriver to the sediments of Youngs Bay.

Benthic Algae

The most abundant group of plants associated with the tidal flats of the Columbia River Estuary was the microalgae, which consisted almost entirely of diatoms. Although many diatom species were found on each tidal flat under investigation, the species composition varied greatly among tidal flats. The only other conspicuous group of microalgae was the blue-green algae which were found frequently growing on the sediment beneath the emergent vascular plants of the low marsh in late summer. Macroalgae exhibited a patchy distribution and were relatively rare on the tidal flats of the estuary. *Enteromorpha intestinalis* var. *maxima*, a filamentous green alga, was the only conspicuous macroalga observed at the sampling sites during the study. This taxon was abundant in samples from the low marsh in April and May at sites in Youngs Bay and Baker Bay. Considering the total estuarine area under investigation, the contribution of macroalgae and submergent vascular plants to benthic primary production in the study area was insignificant compared to the productivity of benthic diatoms. Because of the dominance of diatoms in the benthos and because of their potential as indicators of environmental change in the estuary, the species composition of the diatom flora associated with the tidal flats was examined in detail by McIntire and Amspoker (1984).

The dominant diatom taxa in sediment samples from the intensive study site in Baker Bay included brackishwater species (*Navicula diserta* and *N. salinicola*), and euryhaline taxa tolerant of a wide range of salinity (*Achnanthes hauckiana* and *A. lemmermanni*). This flora exhibited very little seasonal change. The occurrence of both brackishwater and freshwater benthic diatoms in the Youngs Bay samples indicated that this site was exposed to intermittent periods of fresh water and brackish water. Seasonal changes in the diatom flora at the site in Youngs Bay were relatively small and primarily related to the relative abundances of freshwater planktonic taxa deposited from the water column. Dominant benthic diatoms in Grays Bay included two freshwater species (*Achnanthes lanceolata* and *Navicula submuralis*), and two salinity-indifferent species (*Achnanthes hauckiana* and *Navicula gregaria*). The dominance of *A. lanceolata* and *N. submuralis* and the occurrence of many other typical freshwater taxa in the samples (e.g., *Achnanthes minutissima*, *Cymbella minuta*, *Gomphonema parvulum* and varieties of *Navicula capitata*) was evidence of the lack of a saltwater influence in the bay. Seasonal changes in the flora at the intensive study site in Grays Bay were greater than at the sites in Youngs Bay and Baker Bay.

The dominant benthic diatoms in the Cathlamet Bay region included *Navicula submuralis*, *Navicula gregaria*, *Fragilaria pinnata*, *Achnanthes* lanceolata, and Amphora ovalis var. pediculus. Among these taxa, N. gregaria is euryhaline and the rest are typical freshwater, stenohaline species. Variations among the samples from the Cathlamet Bay region were primarily related to temporal changes in the flora between spring and early fall. In particular, the planktonic taxon Asterionella formosa was abundant in the benthic samples in May, but decreased in relative abundance during the summer months. This pattern is compatible with the difference in the concentration of this species between the April 1981 and October 1980 planktonic samples obtained from the water column near Tongue Point. Diatom samples also were obtained from a region upriver from Cathlamet Bay. From this region, the sediment samples were collected from three sites on Marsh Island and sites on Horseshoe Island, Brush Island, and Quinns Island. The diatom flora at these sites clearly indicated that this region of the estuary was exposed to freshwater conditions throughout the period of study. Dominant taxa included nine typical freshwater species (e.g., Achnanthes lanceolata, Amphora ovalis, Navicula capitata) and two euryhaline species (Achnanthes hauckiana and Navicula gregaria). Seasonal changes at the Quinns Island site were greater than corresponding changes at the sites in Baker Bay, Youngs Bay, and Grays Bay.

Quantitative analysis of the 56 diatom samples provided the data necessary for classification of the collections into community types. A clustering algorithm (McIntire, 1973) was used to partition the samples into discrete groups relative to the abundance of 44 prominent taxa. The results of this analysis indicated that a five-cluster structure was the most satisfactory for understanding patterns in this particular data set. In Table 7.1 this structure is presented by listing the location and month of each sample by the cluster into which it was grouped. In addition, the regional area from which each sample was obtained is also listed in the table.

Cluster 1 consisted of only one sample, the plankton collection from the water column near Clatsop Spit obtained in October. The diatom community in this sample was unique among the 56 collections and was the only assemblage which contained many typical marine planktonic species. Cluster 2 included all six samples obtained from the intensive study site in Baker Bay. This cluster identified a relatively distinct brackishwater benthic flora, an assemblage with taxa that are often found in the brackish and marine regions of other Oregon estuaries (Amspoker & McIntire, 1978). All samples from the intensive study site in Youngs Bay also were partitioned into a separate cluster (cluster 3). This community consisted of both brackishwater and freshwater benthic diatoms and exhibited a high degree of contamination with freshwater planktonic species. Therefore, this community was best described as a euryhaline benthic assemblage with frequent allochthonous inputs of freshwater benthic and planktonic species. The other 43 samples were grouped into either cluster 4 or cluster 5. Both of these clusters represented freshwater diatom assemblages, but they differed in the degree to which freshwater planktonic species were present. Cluster 5 included the six plankton samples that were dominanted by freshwater species and the benthic samples with a relatively large proportion of freshwater planktonic species. Although some of the benthic samples in cluster 4 contained freshwater planktonic species, these samples were

Table 7.1. Five-cluster structure of the diatom taxon data from the Columbia River Estuary. Regions for benthic data are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB), and Upper Estuary (UE). Locations of plankton samples are Clatsop Spit (CSP), Tongue Point (TPP), Puget Island (PIP), and in the Youngs River (YRP).

Cluster	Sample Site	Month	Region
1	Plankton-Clatsop Spit	October	CSP
2	Baker Bay - Airport Road	April	BB
	Baker Bay - Airport Road	June	BB
	Baker Bay - Airport Road	August	BB
	Baker Bay - Airport Road	October	BB
	Baker Bay - Airport Road	January	BB
	Baker Bay - Airport Road	March	BB
3	Youngs Bay - West Flat	April	YB
	Youngs Bay - West Flat	June	YB
	Youngs Bay - West Flat	August	YB
	Youngs Bay - West Flat	October	YB
	Youngs Bay - West Flat	January	YB
	Youngs Bay - West Flat	March	YB
4	Grays Bay - East Flat	April	GB
	Grays Bay - East Flat	June	GB
	Grays Bay - East Flat	August	GB
	Grays Bay - East Flat	October	GB
	Grays Bay - East Flat	January	GB
	Grays Bay - Middle Sand Bar	June	GB
	Grays Bay - Front Sand Bar	June	GB
	Lois Island - West Tip	June	CB
	Lois Island - West Tip	August	CB
	Lois Island - West Tip	September	CB
	McGregor Island	May	CB
	Grassy Island	June	CB
	Grassy Island	August	CB
	Quinns Island - East Side	April	UE
	Quinns Island - East Side	June	UE
	Marsh Island - West Tip	May	UE
	Brush Island	May	UE
5	Grays Bay - East Flat	March	GB
	Grays Bay - Millers Point	June	GB
	Grays Bay - Portugese Point	June	GB
	Grays Bay - Grays Point	June	GB
	Lois Island - West Tip	May	CB
	Grassy Island	May	CB
	Grassy Island	September	CB
	Russian Island - SW Area	May	CB
	Russian Island - NW Area	May	CB
	Russian Island - SW Area	May	CB
	Quinns Island - East Side	August	UE
	Quinns Island - East Side	October	UE
	Quinns Island - East Side	January	UE
	Quinns Island - East Side	March	UE
	Marsh Island - Sand Bar	May	UE
	Marsh Island - South Flat	May	UE
	Horseshoe Island - SW Flat	May	UE
	Horseshoe Island - SW Flat	July	UE
	Horseshoe Island - SW Flat	August	UE
	Horseshoe Island - SW Flat	September	UE
	Plankton - Puget Island	October	PIP
	Plankton - Tongue Point	October	TPP
	Plankton - Tongue Point	April	TPP
	Plankton - Clatsop Spit	April	TPP
	Plankton - Youngs River	November	YRP
	Plankton - Youngs River	April	YRP

less contaminated by allochthonous inputs from the water column than the benthic samples in cluster 5. None of the plankton samples were classified into cluster 4. The fact that over 75% of the samples were classified into either cluster 4 or cluster 5 was indicative of the strong influence of fresh water in the Columbia River Estuary.

Because a cluster analysis forces entities into discrete groups it was necessary to examine the affinities among the clusters in order to complete a satisfactory interpretation. A canonical analysis of discriminance, a multivariate statistical procedure (Pimental, 1979), provided a useful approach for the graphic display of the results of the cluster analysis, in relatively few dimensions with minimal loss of information. While this method is complex mathematically, the result was a simple two-dimensional graph of the cluster orientation (Figure 7.7). In this case, the two dimensions retained 97.6% of the among-cluster variation. The first axis (axis 1) indicated the large difference between the plankton assemblage from the water column near Clatsop Spit collected in October (cluster 1), and the benthic assemblage of brackishwater taxa in Baker Bay (cluster 2). Although samples from these two clusters were obtained from locations exposed to a similar salinity range, the fragile, marine planktonic taxa were not found in the sediment samples from Baker Bay. It is not clear whether the lack of marine planktonic diatoms in the benthic samples was due to the patterns of circulation in the estuary or to the rapid deterioration of the thin silica frustules characteristic of these species. The marine planktonic assemblage (cluster 1) was more similar to the freshwater assemblages (clusters 4 and 5) than to the brackishwater assemblages from Baker Bay (cluster 2). The absence of freshwater planktonic species in the Baker Bay samples was consistent with the transport of most of the river water out of the estuary through the south channel (see Chapter 3). Figure 7.7 also illustrated the similarity between clusters 4 and 5. As indicated above, these were freshwater assemblages that differed only with respect to the relative abundances of planktonic species.

Axis 2 contrasted the Youngs Bay diatom flora (cluster 3) with the rest of the samples (Figure 7.7). The assemblage in Youngs Bay was distinct, yet showed a greater affinity to the freshwater assemblages than to the brackishwater assemblage in Baker Bay.

It is often informative to examine similarities among diatom assemblages pooled by geographical region. For this purpose the SIMI index of similarity was used, where

$$\mathrm{SIMI} = \left(\sum_{i=1}^{s} p_{1i}p_{2i}\right) \div \left(\sum_{i=1}^{s} p_{2i}^{2} \sum_{i=1}^{s} p_{2i}^{2}\right)^{\frac{1}{2}}$$

Here p_{1i} and p_{2i} are the proportions of individuals represented by the i-th taxon in samples 1 and 2, respectively; and SIMI is the degree of similarity between samples 1 and 2. SIMI varies from zero, when the samples have no taxa in common, to one, when both samples have the same species composition and relative abundance. Table 7.2 shows all

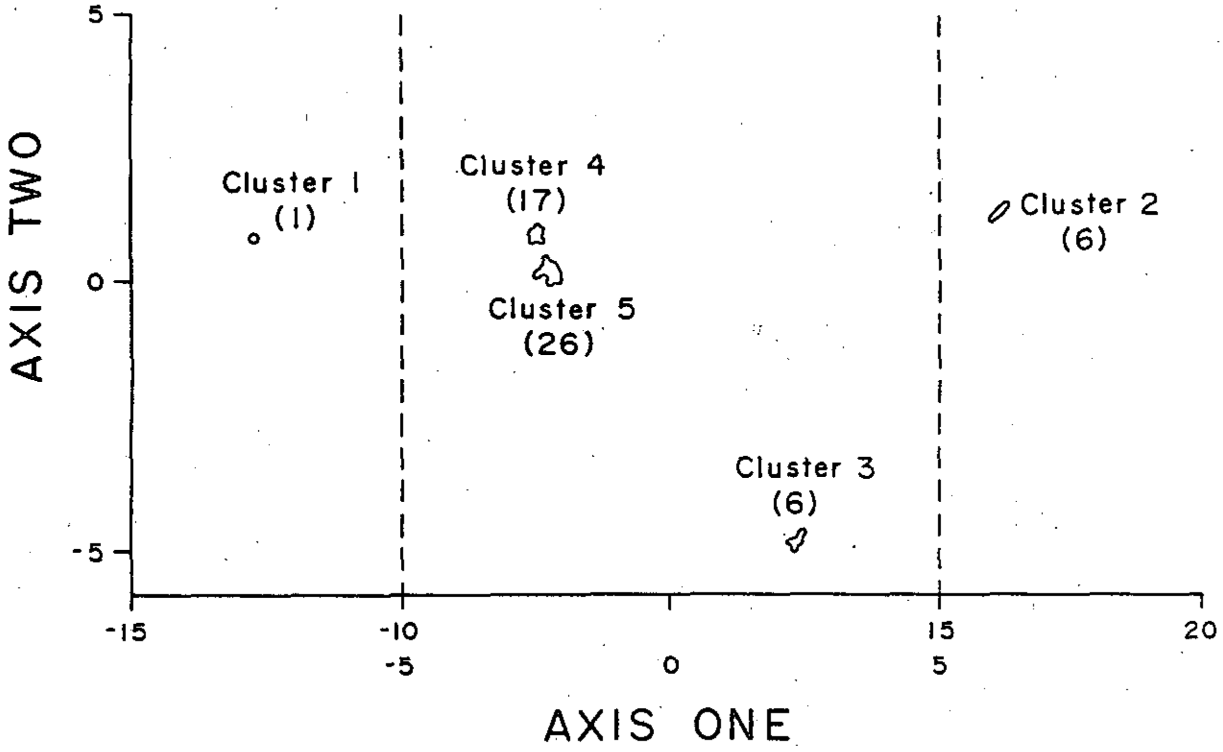


Figure 7.7. Orientation of the five-cluster structure of the diatom data from the Columbia River Estuary. Numbers under each cluster designation indicate the number of samples in a particular cluster.

Table 7.2. A matrix of SIMI values indicating (1) similarity between benthic algal samples from locations where samples pooled by region; (2) similarity between pooled samples from each region and the pooled samples from locations where phytoplankton were obtained; and (3) similarities between phytoplankton samples pooled by collection site. The benthic algal sampling regions are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB) and Upper Estuary (UE). Plankton samples are from the water column near Clatsop Spit (CSP), Tongue Point (TPP), Puget Island (PIP) and in the Youngs River (YRP).

	BB	YB	CB	GB	UE	CSP	TPP	PIP	YRP
YB	0.367								
CB	0.201	0.472							
GB	0.083	0.402	0.854						
UE	0.230	0.677	0.845	0.790					
CSP	0.028	0.519	0.371	0.430	0.581				
TPP	0.015	0.731	0.349	0.410	0.578	0.669			
PIP	0.006	0.523	0.147	0.114	0.255	0.299	0.717		
YRP	0.134	0.544	0.286	0.313	0.513	0.309	0.394	0.225	

possible comparisons among pooled samples from five benthic algal sampling regions, and comparisons between these samples and the plankton samples pooled by site location. The triangular matrix is partitioned into three parts: 1) interregional comparisons for the benthic algal sites; 2) comparisons among pooled plankton samples; and 3) comparisons between regional benthic samples and pooled plankton samples. The conclusions from this analysis supported earlier conclusions:

1. The benthic diatom floras from the Cathlamet Bay, Grays Bay and Upper Estuary regions were similar, and were freshwater floras.

2. The Youngs Bay benthic diatom flora was more similar to the flora from the three freshwater regions than to the flora from Baker Bay, a pattern apparently related to freshwater input from the Columbia River, the Lewis and Clark Rivers, and the Youngs River.

3. Similarity between the benthic floras from the three freshwater regions and the three pooled plankton samples from freshwater locations (Tongue Point, Puget Island, and the Youngs River) was variable and dependent upon inputs to the benthos from the water column.

4. The benthic flora from Youngs Bay was more similar to the floras in the plankton samples than to any of the benthic samples from the other regions except the Upper Estuary, a pattern related to the high relative abundance of Melosira italica in the Youngs Bay and plankton samples.

5. The benthic flora from Baker Bay was dissimilar to the flora in the plankton samples.

6. The planktonic floras from the Puget Island and Tongue Point areas were similar to each other, but less similar to the pooled samples from the Clatsop Spit area.

7. The Youngs River plankton was dissimilar to the plankton from the locations near Clatsop Spit, Tongue Point, and Puget Island. This dissimilarity was related to the presence of many benthic taxa in the plankton from the Youngs River, which did not appear in the other plankton samples from the Columbia River.

Vascular Plants

It is convenient to partition the vascular plant vegetation of the Columbia River Estuary into submergent species associated with the sediments of the intertidal and subtidal zones, and emergent species that comprise the marshlands and swamplands. Submergent vascular plants exhibit a patchy distribution and are relatively rare on the tidal flats of the estuary. In contrast, the emergent vegetation is abundant over an area of approximately 14,500 acres, 2,100 acres of which are exposed to brackish water and 12,400 acres of which are in freshwater regions (Macdonald and Winfield, 1984). In a recent survey of the vascular plant flora of the estuary, Thomas (1983) found 165 species of vascular plants in the region corresponding to the first 40 river miles. Of

Table 7.3. Six cluster structure of the vascular plant data from the Columbia River Estuary. Locations correspond to sampling sites for emergent vascular plants, and descriptions are based on subjective evaluations.

Cluster	Location	Year	Description
1	Baker Bay - China Cove	1980	*Carex* Low Marsh
	Baker Bay - China Cove	1981	*Carex* Low Marsh
	Baker Bay - China Cove	1980	*Scirpus* Low Marsh
	Baker Bay - China Cove	1981	*Scirpus* Low Marsh
	Baker Bay - Ilwaco Harbor	1980	Low Marsh
	Baker Bay - Ilwaco Harbor	1981	Low Marsh
	Trestle Bay - West	1980	Low Marsh
	Trestle Bay - West	1981	Low Marsh
	Trestle Bay - East	1980	*Carex* Low Marsh
	Trestle Bay - East	1981	*Carex* Low Marsh
	Youngs Bay - Outer	1980	Low Marsh
	Youngs Bay - Outer	1981	Low Marsh
	Youngs Bay - Inner	1980	Low Marsh
	Youngs Bay - Inner	1981	Low Marsh
	Army Corps Pier (Tongue Point)	1980	Low Marsh
	Grays Bay - Outer	1980	Low Marsh
	Grays Bay - Outer	1980	High Marsh
	Karlson Island	1980	Low Marsh
	Quinns Island	1980	Low Marsh
	Quinns Island	1981	Low Marsh
2	Grays Bay - Inner	1980	High Marsh
	Grays Bay - Inner	1981	High Marsh
	Grays Bay - Outer	1981	High Marsh
	Russian Island	1980	High Marsh
	Russian Island	1981	High Marsh
	Tronson Island	1980	High Marsh
	Tronson Island	1981	High Marsh
3	Lois Island	1980	Low Marsh
	Lois Island	1981	Low Marsh
	Grays Bay - Inner	1980	Low Marsh
	Grays Bay - Inner	1981	Low Marsh
	Grays Bay - Outer	1981	Low Marsh
	Karlson Island	1981	Low Marsh
4	Puget Island	1981	Typha Marsh
5	Army Corps Pier (Tongue Point)	1981	Low Marsh
6	Trestle Bay - West	1980	High Marsh
	Trestle Bay - West	1981	High Marsh
	Trestle Bay - East	1980	Low Marsh
	Trestle Bay - East	1981	Low Marsh
	Trestle Bay - East	1980	Mid Marsh
	Trestle Bay - East	1981	Mid Marsh
	Trestle Bay - East	1980	High Marsh
	Trestle Bay - East	1981	High Marsh

these species, only 11 were associated with the tidal flats and subtidal regions.

The clustering approach described above for the benthic diatom data provided a satisfactory analysis of the vascular plant data set. A six-cluster structure generated by the clustering algorithm was the most interpretable pattern in the vascular plant data matrix (Table 7.3). Cluster 1 consisted primarily of low marsh sites in brackish water. However, the dominance of Carex lyngbyei, a euryhaline species, at four sites in the middle estuary grouped these samples with the brackish water sites. Other taxa predominant in some of the samples of cluster 1 included Triglochin maritimum, Scirpus americanus, and Eleocharis palustris. Cluster 2 included seven samples from high marsh sites in the middle of the study area. Some of the dominant taxa in these samples were Oenanthe sarmentosa, Lotus corniculatus, Mimulus guttatus, Carex lyngbyei, and Deschampsia caespitosa. Samples from low marsh sites in the middle of the study area were the six components of cluster 3. Again, Carex lyngbyei was abundant in all of these samples. Other dominant taxa associated with cluster 3 included Alisma plantago-aquatica, Sagittaria latifolia, Eleocharis palustris, and Juncus oxymeris. Clusters 4 and 5 were one-sample clusters which were separated from the other groups on the basis of several dominant taxa. Cluster 4 represented a marsh on Puget Island dominated by Typha latifolia, whereas cluster 5 was a sample from a low marsh near Tongue Point where Myosotis laxa and Equisetum sp. were abundant. The latter taxon also was abundant in one sample from Youngs Bay and two samples from Grays Bay. Cluster 6 was composed of eight samples from Trestle Bay, only two of which were from the low marsh. The abundant species in these samples were Lathyrus palustris, Potentilla pacifica, Carex lyngbyei, Juncus balticus, and Agrostis alba.

A canonical analysis of discriminance allowed the cluster structure of Table 7.3 to be displayed in two dimensions (Figure 7.8). These two axes retained 88.2% of the among-group variation, while illustrating the clustering orientation in one simple graph. In this diagram the brackishwater groups (clusters 1 and 6) were relatively close, while the discrete and unique nature of the high marsh samples from the middle of the study area was apparent. The low marsh samples from the mid-region and the sample from the Typha marsh on Puget Island (clusters 3 and 4) had a greater affinity for the brackishwater clusters than for cluster 2. These relationships were indicative of the presence of a few euryhaline species that were abundant at both brackishwater and freshwater locations. Cluster 5, dominated by Myosotis laxa, Carex lyngbyei, Eleocharis palustris, Juncus oxymeris, Equisetum sp., and Isoetes echinospora, was well separated from all the other clusters. Of these taxa, M. laxa and I. echinospora were primarily responsible for this separation.

The cluster structure of the vascular plant data (Table 7.3) corresponded to some of the habitat types proposed by Thomas (1983). In particular, clusters 1,2,3, and 6 were roughly representative of Thomas' brackishwater low marsh, freshwater high marsh, freshwater low marsh and brackishwater high marsh, respectively.

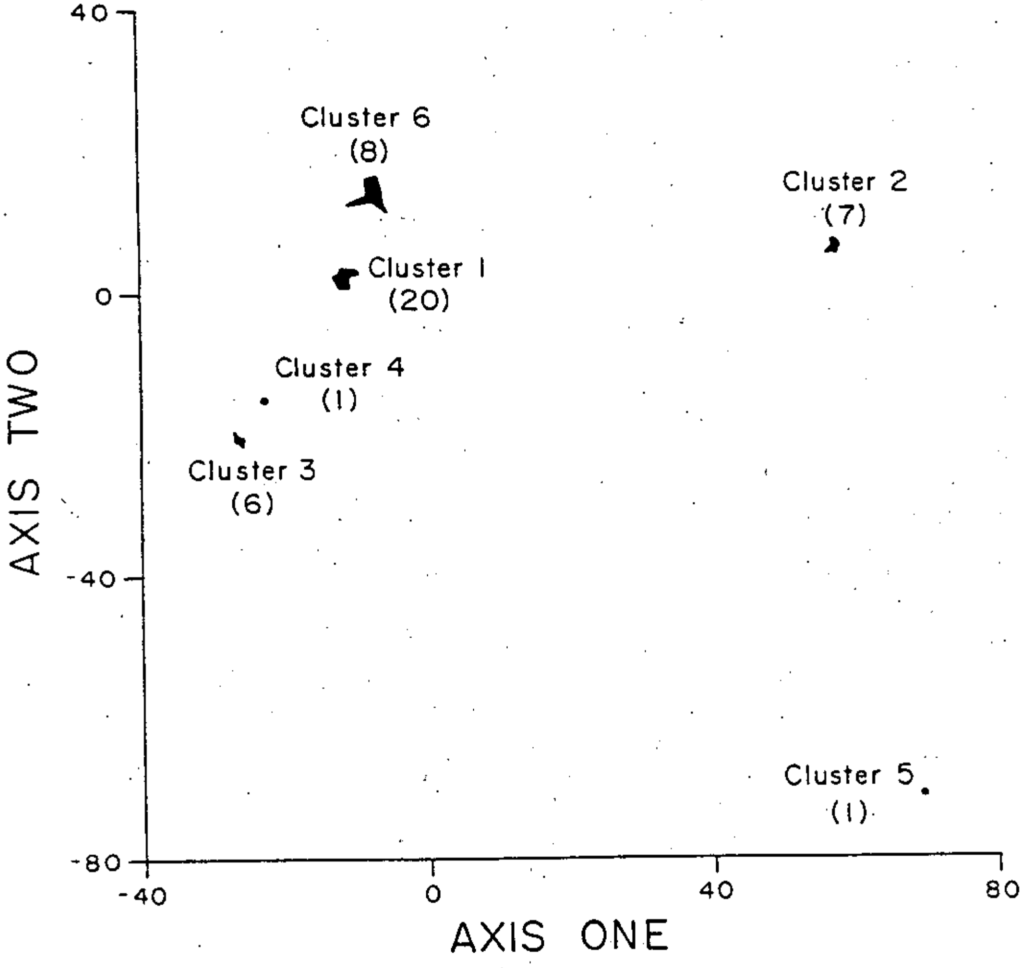


Figure 7.8. Orientation of the six-cluster structure of the vascular plant data from the Columbia River Estuary. Numbers under each cluster designation indicate the number of samples in a particular cluster.

7.1.3 Biomass

The state variables in Figure 7.2 represent the biomasses of phytoplankton, benthic algae, and vascular plants. Benthic macroalgae and submergent vascular plants comprise such a small fraction of the total plant biomass of the Columbia River Estuary that they were ignored for purposes of this study.

Phytoplankton

Quantitative evaluation of the living phytoplankton biomass was done by Frey et al. (1984), in terms of the chlorophyll a content of particles filtered onto membrane filters (Strickland and Parsons 1972), and in terms of carbon, through development of an acceptable carbon/chlorophyll a ratio.

Distribution of chlorophyll a was averaged over the water column by region for the main body of the estuary (regions 1, 3 + 5, 7 and 8) (Figure 7.9) and for the bays and tributary rivers (regions 4, 6, 9 and 10) (Figure 7.10). Distribution in the main body of the estuary showed prominent seasonal changes as well as rapid decreases from the Fluvial Region to the Entrance Region (Figure 7.9). Of particular note was the pronounced decrease in chlorophyll concentration between region 7 and region 3 + 5 in late spring and summer (May and July, 1980). The April 1981 data also showed this pronounced decrease. The interface between regions 3 + 5 and 7 coincided with the area in which freshwater diatoms were lost from the water column (Figure 7.6), but was generally upriver from the near-bottom turbidity maximum at this time of year (Sherwood et al. 1984). Haertel (1970) reported that chlorophyll a decreased downstream with increasing salinity, but did not note an extreme threshold between upriver and downriver concentrations (perhaps because of the lack of sample density). In June 1982 remote sensing techniques from an airplane detected a downstream chlorophyll decline, but resolution was too low for delineation of a threshold in the Tongue Point area (Bristow et al., in preparation).

The bays and tributary rivers also showed a seasonal pattern in chlorophyll a concentration (Figure 7.10). In most cases, during the period from spring through fall, the bays had lower chlorophyll concentrations than the small rivers that flowed into them, suggesting that freshwater phytoplankton in the rivers did not carry over into the more brackish water of the bays. This pattern was not observed during the winter months.

At three stations at different times of year, the phytoplankton was size-fractionated by filtering water samples with endemic phytoplankton through both 33 um-mesh and 10 um-mesh nylon monofilament netting. This gave phytoplankton size fractions larger than 33 um, smaller than 10 um, and between 10 and 33 um, all of which were analyzed for chlorophyll a content. The chlorophyll a concentrations representing each size fraction changed somewhat differently relative to one another as the seasons progressed (Figure 7.11). Highest values were noted in spring and summer for all three size groups, but the greatest increase during the spring and summer was noted in the cell fraction larger than 33 um.

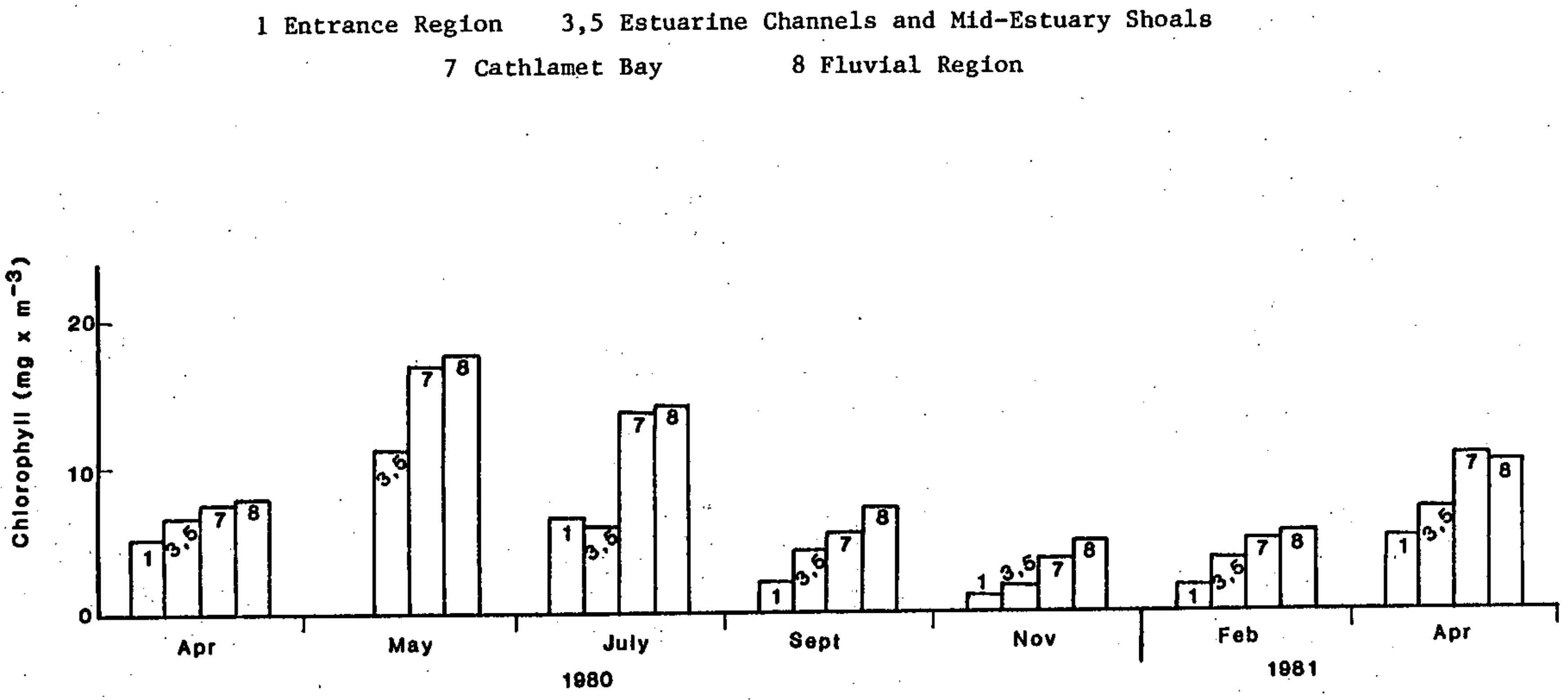


Figure 7.9. Mean chlorophyll a concentrations (mg m^{-3}) by sampling months and by regions for the main body of the Columbia River Estuary. May 1980 concentrations reflect the eruption of Mount St. Helens to some unknown extent.

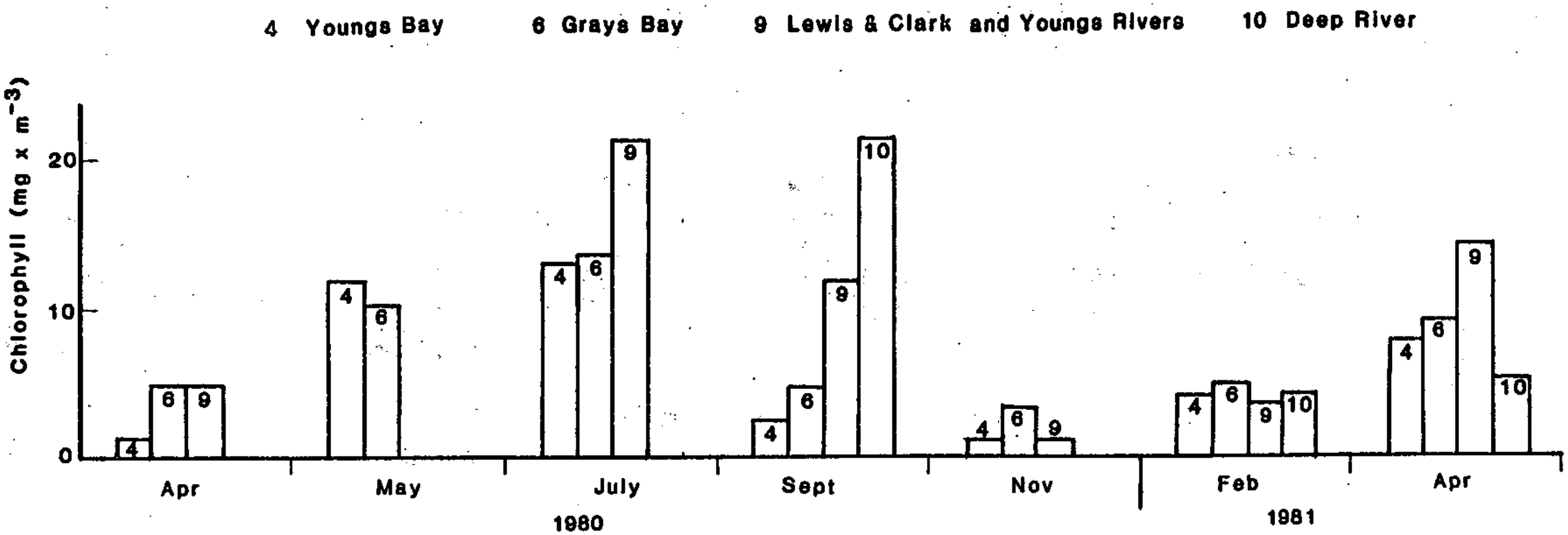


Figure 7.10. Mean chlorophyll a concentrations in bays and tributary rivers. May 1980 concentrations reflect the eruption of Mount St. Helens to some unknown extent.

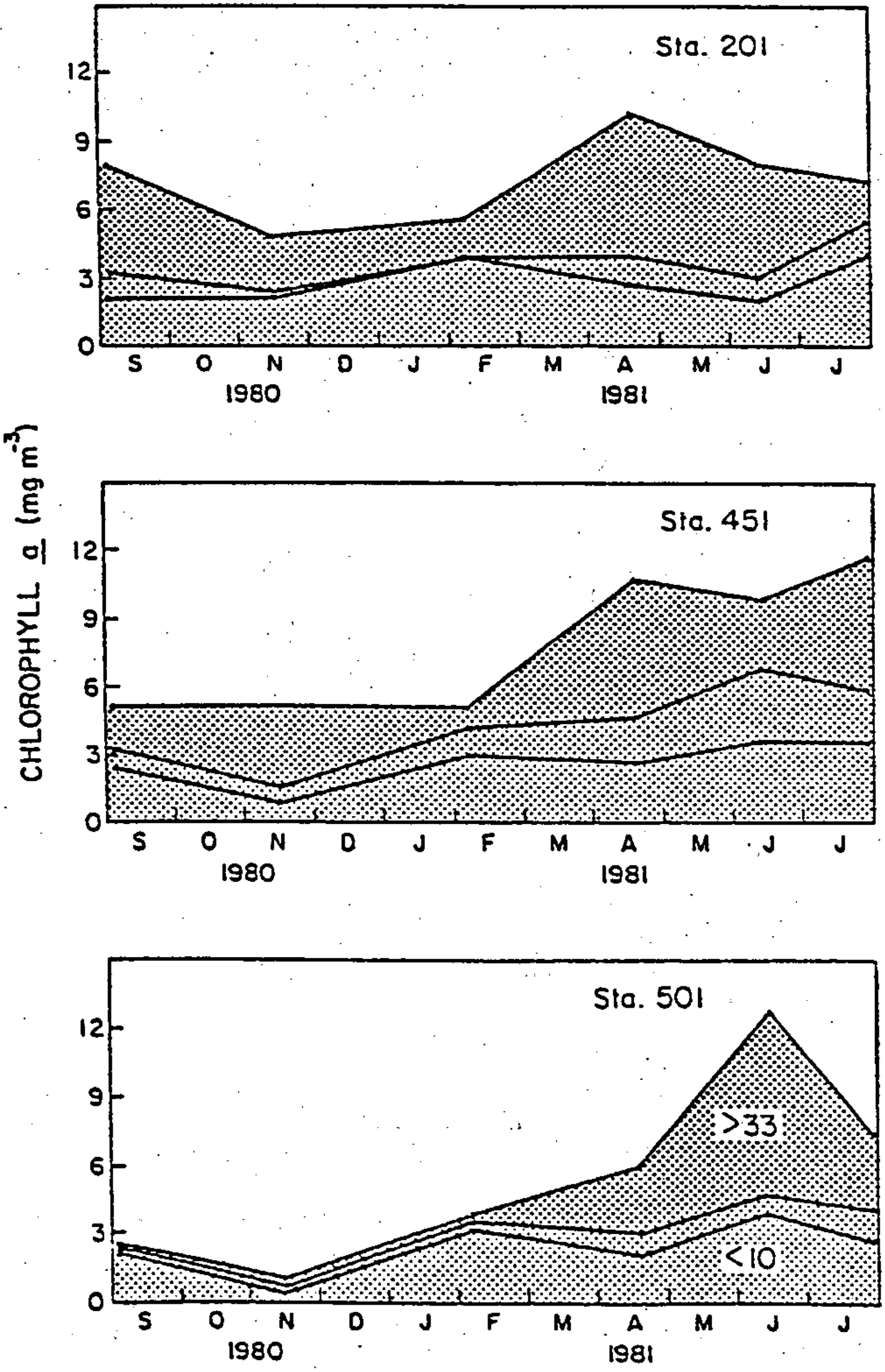


Figure 7.11. Chlorophyll a content (mg m^{-3}) of three size fractions of phytoplankton (<33 µm, 10-33 µm, and 10 µm) at three stations in the main body of the Columbia River Estuary.

This size group mainly contained the larger diatoms, which always became prevalent in spring and continued to dominate through the summer. The second most abundant size group was the group with the smallest cells (10 um). These cells were mainly freshwater microflagellates. The least abundant size group was composed of cells between 10 and 33 um. Chlorophyll *a* concentration in all three size fractions was lowest in winter at the most seaward of the three stations (Station 501, Figure 7.11). In the spring and summer the concentration increased at all stations, mainly the result of cells greater than 33 um and less than 10 um. The June peak at Station 501 was related to the proliferation of mostly marine and brackishwater diatoms at this time of year, while the broad temporal increases in April through July at Stations 451 and 201 reflected increases in freshwater populations.

Phytoplankton biomass was well mixed from surface to near bottom at all times of the year at all stations in the bays and tributary rivers and the main body of the estuary, except in the Entrance Region, where chlorophyll *a* varied with depth as a result of the intrusion of ocean water with the flood tide (Frey et al, 1984). In the Entrance Region, the upper waters (upper 5 m) were richest in chlorophyll *a* during summer, but near-bottom waters were slightly richer in mid-winter. Nearly complete vertical mixing can occur at flood tide in late winter and spring in the Entrance Region. The general picture of water-column chlorophyll *a* distribution in spring and summer, therefore, is one of little to no vertical structure (except near the estuary mouth, in the main body of the estuary), but a pronounced horizontal gradient between relatively high chlorophyll *a* concentrations upriver of Tongue Point and lower concentrations below Tongue Point. In winter, the horizontal gradient from upriver to the sea persists, but apparently without the sharp discontinuity in the Tongue Point region.

One explanation for the decline in chlorophyll *a* concentration from fresh water to marine water in the main body of the estuary was that it was an artifact caused by time of sampling during each sampling day. Chlorophyll *a* content of plant cells can vary systematically with time of day (Lorenzen, 1963; Wood and Corcoran, 1966; Yentsch and Scagel, 1958; Glooschenko, *et al*, 1972). Frey et al. (1984) discounted systematic diel variation, however, as no pattern emerged when chlorophyll *a* concentrations in samples from stations along the estuary at different seasons were plotted against the time of day that the sample was obtained. A second explanation for the horizontal chlorophyll gradient was that riverine waters with high chlorophyll concentrations mixed with marine-derived water containing less chlorophyll *a*, to yield a dilution in the mixing and marine zones. If chlorophyll *a* were behaving as a conservative property affected only by dilution processes, and if chlorophyll *a* in the river and salinity in the ocean were constant in time, linear decrease in chlorophyll should be observed in a plot of chlorophyll *a* against salinity. However, a linear relationship was not apparent (Figure 7.12). The chlorophyll *a* decrease was much more rapid than that predicted by a dilution model. Strictly speaking, neither the chlorophyll *a* in the river nor the salinity in ocean source water is ever constant through time; however, the deviations of the data points from the predicted dilution curves in Figure 7.12 were so great that dilution seemed a highly improbable

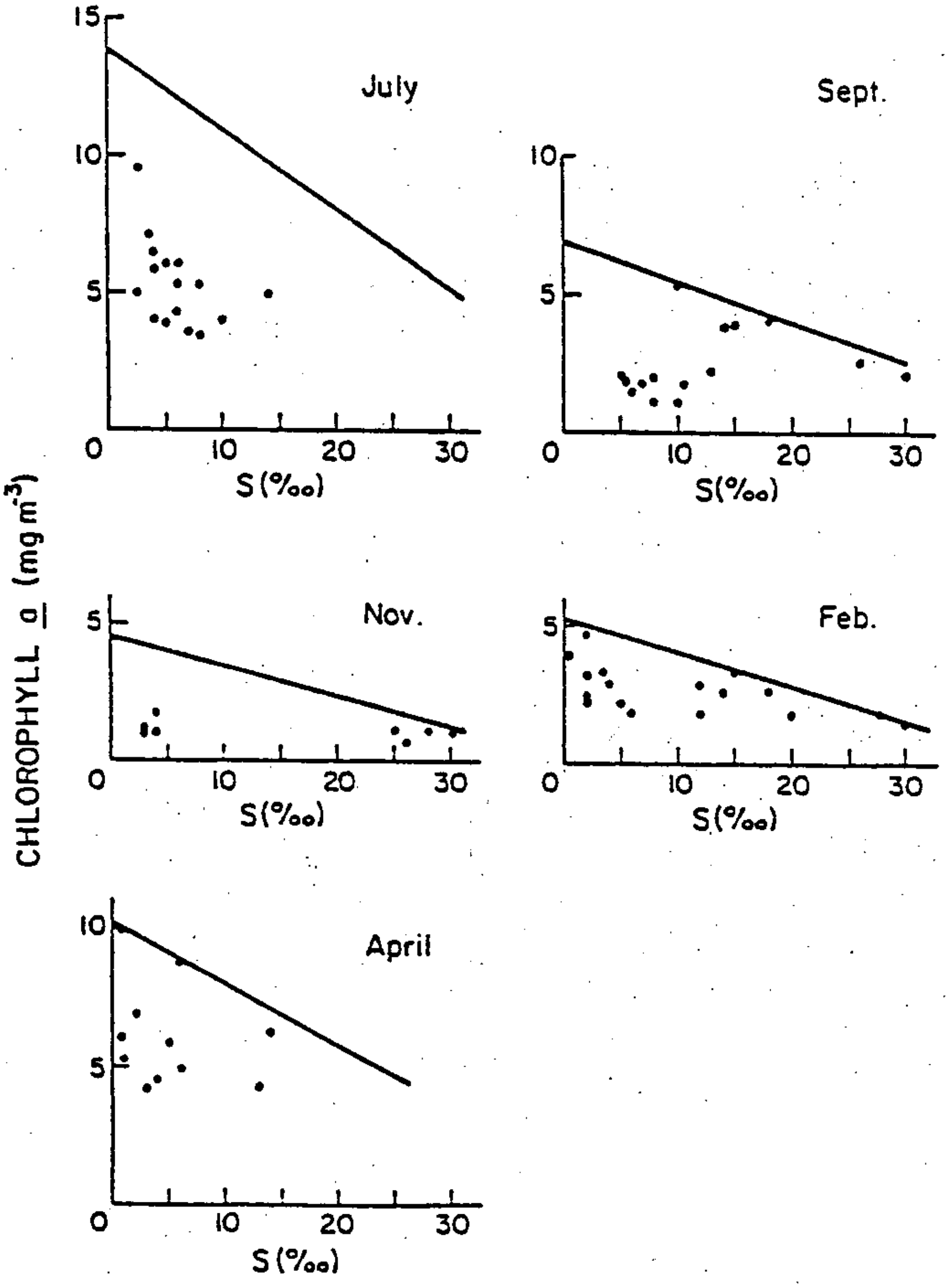


Figure 7.12. Chlorophyll a concentration (mg m^{-3}) as a function of salinity. Straight lines represent the relationship if chlorophyll a had decreased solely as a function of dilution of riverine water with seawater.

explanation for the horizontal distribution of chlorophyll a in the main body of the estuary.

All evidence supports the hypothesis that freshwater phytoplankton undergo rapid plasmolysis as they encounter osmotic changes brought on by increasing salinity. Such cells either disappear rapidly from the water column by sinking or disintegrating, or simply lose their chlorophyll a, thereby causing the observed losses of chlorophyll a in a downstream direction. The rapid decrease in abundance of nine freshwater diatom species as they encountered slightly saline water (Figure 7.6) supports the idea that whole cells were removed from the water column. Chlorophyll a might have been lost from cells as they were removed, and the non-pigmented remains of the cells might have been re-mixed into the water column for eventual transport downstream. There was no extraordinary accumulation of organic matter on the estuary bottom in the Tongue Point region but there was an accumulation of bottom fauna which could have been grazing a portion of the settled cells (see Section 7.3). There was no direct evidence to link the disappearance of phytoplankton cells at the surface with the shifting turbidity maximum near the estuary bottom (see Chapter 4).

Phytoplankton biomass in terms of chlorophyll a can be converted to biomass in terms of carbon if an acceptable carbon/chlorophyll a ratio (C/CHLOR) can be generated. Frey et al. (1984) calculated a C/CHLOR ratio ranging from 20 to 50 for the Columbia River Estuary, with a mean value of 40. This ratio was similar to previously reported values. For example, Strickland (1960) suggested a ratio of 30, Heinle and Flemer (1975) obtained a ratio of 50 for the Patuxent River Estuary, Kremer and Nixon (1978) found a ratio of 30 for Narragansett Bay and Chervin (1978) obtained a range of ratios from 46 to 72 for the lower Hudson River Estuary. To estimate phytoplankton carbon biomass anywhere in the Columbia River Estuary, the chlorophyll a concentrations were multiplied by the C/CHLOR ratio of 40.

Benthic Algae

The benthic algae of the Columbia River Estuary consist almost entirely of benthic diatoms and planktonic diatoms that have been deposited in the sediment from the water column. The autotrophic biomass associated with the tidal flats was expressed as the concentration of chlorophyll a in the top centimeter of sediment (McIntire and Amspoker 1984). Concentrations at the 4.5-5.5 cm and 9-10 cm depths also were measured and compared to the concentration near the surface as an indication of vertical mixing in the sediments.

Recently Davis and McIntire (1983) established a ratio between microalgal biomass expressed as ash-free dry weight and the concentration of chlorophyll a associated with that biomass (AFDW/CHLOR). AFDW/CHLOR values varied from about 108 to 255, with a mean for all experiments of 167 and a standard error of abount 8. Although the samples for the experiments were obtained from a tidal flat in Yaquina Bay near Newport, Oregon, these ratios represent the best estimates available for converting the chlorophyll data from the Columbia River Estuary to estimates of autotrophic biomass. If it is assumed that one-half of the biomass was carbon, the mean ratio of organic carbon to chlorophyll a, based on these experiments, was 83.5, a value about twice the ratio estimated for the phytoplankton. The value of 83.5 fall within the range of 10.2 to 153.9 reported by Jonge (1980).

Microalgal chlorophyll-based biomass data collected at the five intensive study sites (Figure 7.4) are summarized in Table 7.4. The mean concentration of chlorophyll a in the top cm of sediment for the five pooled study sites exhibited relatively little seasonal change, varying from a minimum of 11.8 ug cm^{-3} in March 1981 to a maximum of 19.2 ug cm^{-3} in November 1980. The mean value of all observations obtained from the top cm of sediment was 15.2 ug cm^{-3} (Table 7.4). Mean values for observations pooled by intensive study site ranged from 1.4 ug cm^{-3} for the Clatsop Spit site to 26.4 ug cm^{-3} for the Youngs Bay site. If it is assumed that the chlorophyll concentration is a reliable index to the capacity for benthic autotrophy, these data indicate that the most productive sites were Youngs Bay and Baker Bay. The sites at Grays Bay and Quinns Island had a productive capacity about 40% of the capacities at Youngs Bay and Baker Bay. The extremely low productive capacity at the Clatsop Spit site was apparently related to the stability and properties of the sediment in that area. On the average, sediments near the surface had the highest concentration of chlorophyll a along the marsh transect, followed by the upper, mid and lower intertidal transects, in that order. In general, the lower transects were exposed more to physical disruption from water movements and to lower light intensities than the transects nearer the low marsh. The patterns that emerged from the analysis of data from the 31 survey sites (Figure 7.4) were consistent with the data obtained at the intensive study sites. (McIntire and Amspoker 1984).

Vascular Plants

Biomasses of above-ground material from emergent vascular plants consist of live stems, leaves and inflorescences plus any attached dead material from the same season's growth. This above-ground vegetation provides food and shelter for wetland herbivores, and contributes greatly to the detrital pool when it dies back each autumn. The below-ground matter provides the basic stock from which the following year's vegetative growth arises.

Above-ground biomass concentrations during five sampling months in 1980 are given in Table 7.5 for high-, low-, and mid-marsh regions in each of the sampling sites (Figure 7.5). Carbon biomass can be computed approximately as 40% of dry weight (Macdonald and Winfield 1984). Peak biomasses occurred in either June or July at all sampling sites. These biomass values were similar to a peak biomass of 687 g dry weight m^{-2} recorded in a Carex-dominated tidal marsh in the Fraser River Estuary, B.C. (Kistritz, et al. 1983). Except for the Trestle Bay site, the high marsh contained a greater biomass than the adjacent low marsh during the peak biomass period, in regions where both marsh areas were represented. It should be noted that substantial biomass was still present at most sites in October, although a great fraction of this biomass was dead by that time of year. By winter most of this marsh vegetation was gone.

Table 7.4 Mean concentrations of chlorophyll a (ug cm^{-3}), sample sizes and standard error of the means for five intensive study sites in the Columbia River Estuary. Data pooled by sampling time (month), site, and tidal level (transect) represent means of measurements in the top cm of sediment. Data pooled by sediment depth represent means of all observations for the top cm of sediment and at depths 4.5-5.5 cm and 9-10 cm below the surface.

Variable	Sample Size	Mean	Standard Error
Time:			
April	90	17.6	1.5
May	114	17.8	1.1
June	114	19.0	1.4
July	114	13.7	0.9
August	114	14.3	1.0
September	114	17.5	1.7
October	114	15.2	1.2
November	48	19.2	1.9
January	96	13.1	1.3
February	114	13.8	1.3
March	114	11.8	1.0
April	114	12.2	1.0
Site:			
Clatsop Spit	204	1.4	0.1
Youngs Bay	270	26.4	0.8
Baker Bay	270	25.1	0.7
Grays Bay	252	10.3	0.4
Quinns Island	264	9.0	0.5
Tidal Level Transect:			
Marsh (0.9m above MLLW)	258	21.0	0.7
Upper (0.7m above MLLW)	354	16.1	0.8
Mid (0.5m above MLLW)	336	14.0	0.7
Lower (0.3m above MLLW)	312	10.7	0.5
Sediment Depth:			
Top cm	1260	15.2	0.4
4.5-5.5 cm	798	8.1	0.2
9-10 cm	798	5.2	0.2

Table 7.5. Mean live and attached dead marsh plant above-ground biomass (g dry wt/m^2) in 1980. L=Low marsh, H=High marsh, M=Middle marsh.

	APRIL		MAY		JUNE		JULY		OCTOBER	
	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD	LIVE	DEAD
Baker Bay:										
China Cove *Carex* (L)	68	5	575	26	821	52	523	108	226	382
China Cove *Scirpus* (L)	29	4	340	2	386	36	356	117	39	228
Ilwaco (L)	32	9	622	8	597	29	717	128	237	429
Trestle Bay:										
West (L)	191	18	645	0	794	49	545	55	196	224
West (H)	250	40	509	12	782	43	730	87	485	227
East *Carex* (L)	140	12	479	19	1,089	48	1,417	313	10	148
East (L)	101	9	320	0	706	28	679	102	460	179
East (M)	429	41	540	6	279	26	816	84	487	190
East (H)	125	32	445	0	551	24	639	132	176	229
Youngs Bay:										
Outer (L)	136	14	924	100	2,358	170	1,646	323	479	631
Inner (L)	136	10	433	23	718	113	772	209	156	221
Grays Bay:										
Outer (L)	-	-	317	4	416	28	555	86	186	48
Outer (H)	126	8	470	0	971	26	700	120	402	184
Inner (L)	90	13	476	3	319	16	316	75	290	95
Inner (H)	171	5	573	9	1,021	83	839	54	479	265
Cathlamet Bay:										
Army Corps Dock (L)	48	10	536	0	595	32	822	80	192	97
Lois Island (L)	7	1	204	0	331	33	274	36	28	16
Russian Island (H)	26	1	419	0	819	53	959	134	232	312
Karlson Island (L)	28	3	114	2	547	20	527	49	268	85
Tronson Island (H)	77	12	295	13	712	56	539	53	223	66
Fluvial Zone:										
Quinns Island (L)	30	2	342	20	624	49	701	77	153	47
Puget Island (H)	-	-	-	-	-	-	1,383	119	-	-

Above-ground vegetation began to re-appear in March or April.

Below-ground biomass did not show the seasonal changes of the above-ground biomass (McDonald and Winfield 1984). In some areas there appeared to be greater below-ground biomass in October than in summer, which might indicate downward translocation of organic compounds from above-ground vegetation to the rhizomes and roots. This pattern seemed particularly pronounced in the *Carex*- and *Scirpus*-dominated areas. Kistritz et al. (1983) found that 38% of the peak standing stock was translocated into roots in the *Carex*-dominated tidal marsh in the Fraser River Estuary.

7.1.4 Resource Inputs and Controlling Physical Variables

Light and nutrient inputs are resources coupled to the Primary Production process, while temperature, salinity, sediment properties, and frequency and duration of tidal submergence are variables which help control Primary Production but do not contribute matter or energy (Figure 7.2).

Light Inputs

Photosynthetically active solar radiation (295-695 nm wavelength range) incident to the water surface was measured with a precision spectral pyranometer in units of gcal cm^{-2} day^{-1} (Frey et al. 1984). The monthly mean light input in the vicinity of Astoria, Oregon, is shown in Figure 7.13. Incoming solar radiation ranged from a mean of 47 gcal cm^{-2} day^{-1} in December 1980 to a mean of 240 gcal cm^{-2} day^{-1} in July 1980.

Light penetration into the water column also was measured, and the diffuse light attenuation coefficient (*k*) was calculated in units of m^{-1}. The range of *k* values for the main body of the estuary was approximately 1 to 3 throughout the year, except after the volcanic eruption in May 1980, when values up to 8 were calculated (Frey et al. 1984). High *k* values indicated very shallow photic depths and probable light limitation of the phytoplankton stock. The depth of light penetration to 1% of surface intensity in the mixing zone in December 1980 averaged about 1 m, for example, and it rarely exceeded 4 m even in the clearest water in the marine zone in early spring. This means that a phytoplankton cell mixed through a 10m water depth in the mixing zone in December would be in the light field in the top meter of water only about 10% of each daylight period. In December the daylight period available for photosynthesis is about eight hours; thus, on a 24-hour basis, phytoplankton in the mixing zone might receive photosynthetically active radiation only about 3% of the time. Even in midsummer, with longer daylength, more intense radiation input and deeper photic depth, phytoplankton would rarely be exposed to photosynthetically active radiation for periods longer than 5 hrs (20% of the 24-hr day). One week after the Mount St. Helens eruption the photic depth was about 0.5m, which further exacerbated the light availability problem for phytoplankton. Other than during the eruption, *k* values in the bays and tributary rivers ranged from about 2 to 4, depending upon location and time of year. Using a 5m mixing depth as representative for the bays,

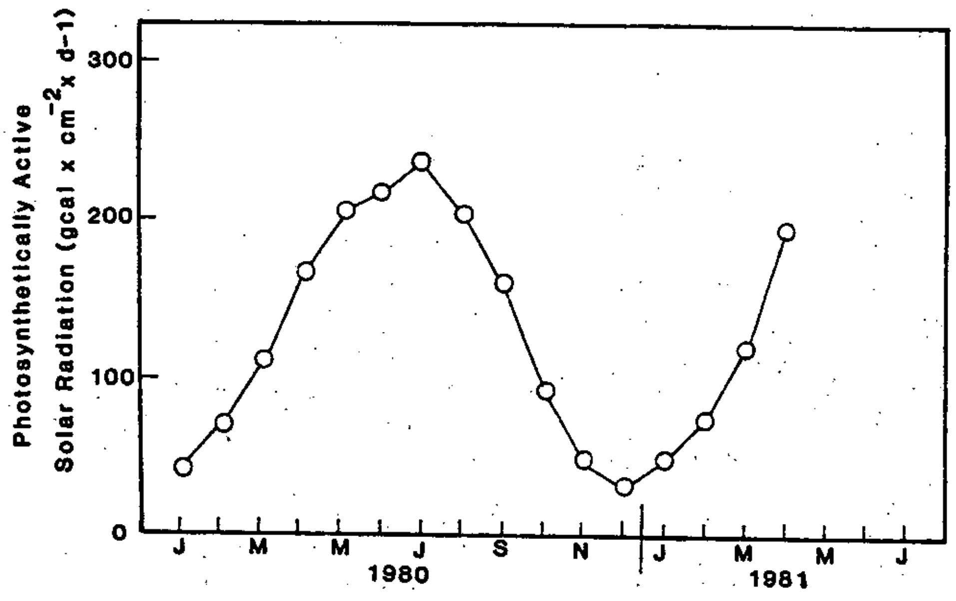


Figure 7.13. Mean monthly averages of photosynthetically active solar radiation at Astoria, Oregon.

the phytoplankton would still only encounter photosynthetically active light about 6% of each 24 hr cycle in winter and about 40% in midsummer. Therefore, light limitation was significant for phytoplankton in the Columbia River Estuary.

The light energy available to microalgal assemblages on the tidal flats of the Columbia River Estuary is determined by 1) day length; 2) the intensity at the sediment surface; and 3) the properties of the sediment. The intensity at the sediment surface is influenced by atmospheric conditions that vary with season, location relative to the patterns of tidal fluctuation and freshwater discharge, and the optical properties of the water mass that periodically or continuously inundates the sediments. Research with diatom assemblages from tidal flats in Netarts Bay near Tillamook, Oregon, indicated that the reduction of photosynthetically active radiation to 1% of the intensity at the sediment surface occurred at 2.6 mm below the sediment surface at a sandy site (mean grain size of 0.21 mm), while the corresponding value for a silty site (mean grain size of 0.07 mm) was 1.3 mm (Davis and McIntire, 1983). Although diatom assemblages from tidal flats reach their maximum rate of photosynthesis at relatively low light intensities, usually between 10% and 20% of full sunlight on a clear day, turbid water with high sediment loads can greatly reduce the period of effective illumination. In fact, the annual mean period per day when light was estimated to be at a saturating intensity for phytosynthesis was only 4.2 hours (17.5% of the 24-hr day) for the benthic intertidal regions of the Columbia River Estuary.

The production dynamics of vascular plants in the marshes and swamps of the estuary are more closely associated with seasonal changes in day length than with hourly fluctuations in light intensity during the daylight periods. Therefore, for vascular plants, the minimum temporal resolution of the light data can be a month (Figure 7.13). The hourly and daily fluctuations in vascular plant photosynthetic rates with changing light intensity were not investigated.

Nutrient Input

Concentrations of dissolved inorganic phosphate, nitrate+nitrite, and silicate were determined for the main body of the estuary and for the bays (Frey et al. 1984). In the main body, highest phosphate and nitrate+nitrite concentrations were found in winter and early spring, and lowest concentrations in the summer. Values of nitrate+nitrite sometimes were lower than 1 uM (equivalent to 14 mg m^{-3}) in midsummer, but ranged upward to greater than 35 uM in early spring. Dissolved silicate did not show the same pattern because of the Mount St. Helens eruption in May 1980. The pyroclastic ashfall and runoff contributed enormous quantities of dissolved silicate to the estuary in May, with concentrations decreasing into summer. Winter concentrations were high as expected, but summer values were unusually high because of the volcanic debris.

Phosphate levels in the bays varied by location, and did not show the consistent temporal pattern observed in the main body of the estuary. However, silicate and nitrate+nitrite concentrations in the bays did show the typical pattern of high concentrations in winter and low concentrations in summer. Nitrate+nitrite levels approached zero on some occasions. No other nitrogen forms besides nitrate+nitrite (e.g., ammonium) were measured in the study, so it is not possible to say that total nitrogen available to phytoplankton was zero or near-zero in summer. Furthermore, rates of incorporation of nutrients into phytoplankton were not measured, and therefore nitrogen limitation of phytoplankton growth cannot be assessed. Low nitrogen concentrations in the water need not imply low rates of incorporation into cells. The spring-to-summer decreases in dissolved nitrogen and silicate likely were due in large measure to phytoplankton utilization, however, because there were concomitant spring-to-summer increases in chlorophyll _a_ (Figures 7.9 and 7.10).

Vertical distributions of the three nutrients in the tidal-fluvial zone were always uniform. Near the estuary mouth, however, incursions of seawater often created stratified nutrient distributions (Frey et al. 1984). In the Entrance Region in summer at flood tide, phosphate and nitrate+nitrite concentrations were greater in the incoming saline water near the bottom of the channel than in the riverine water near the surface. The higher concentrations in near bottom water were the result of summer upwelling off the coasts of Oregon and Washington. Silicate concentrations were higher in summer surface waters in 1980 because of the residual effects of Mount St. Helens. The vertical distributions of phosphate and nitrate+nitrite were reversed in winter, with highest concentrations in the overriding riverine water and lowest concentrations in the ocean-derived water near the bottom. Coastal upwelling usually does not occur in winter off Oregon-Washington, and winter rains increase runoff of dissolved nutrients from the watershed into the Columbia River.

The phytoplankton in the study area did not appear to be limited by nutrient supply in 1980-81, nor were the cells likely to have been nutrient-limited in other years. When the annual budgets for the three nutrients in the Columbia River Estuary in 1980-81 were compared to estimates made in previous years, the corresponding values generally were similar (Table 7.6). The 1974 year was one of large runoff, which appeared to increase the annual loads of phosphate and silicic acid in the water, but not nitrate+nitrite. The 1980-81 silicic acid concentration was less than that in 1974, even with the eruption of the volcano in 1980-81.

The sediment chemistry of the tidal flats and channel areas was not investigated in the present study. Consequently, it is impossible to determine whether or not benthic primary production in the estuary was limited at times by nutrient supply. However, recent enrichment experiments at a tidal flat in Yaquina Bay, Oregon (Cardon, 1982) indicated that microalgal growth was not enhanced by the addition of an algal culture medium that contained the nutrients required to support the growth of diatoms (Guillard and Ryther 1962).

Temperature

Water temperature can control rates of metabolism, including

Table 7.6. Annual chemical budgets for the Columbia River in 1966, 1967, 1974, and 1980-1981.

Variable	1966[1]	1967[1]	1974[2]	1980-1981[3]
Water (liters)	2.0×10^{14}	2.3×10^{14}	2.5×10^{14}	2.0×10^{14}
Phosphate (moles)	1.2×10^{8}	0.8×10^{9}	2.8×10^{8}	1.4×10^{8}
Nitrate + Nitrite (moles)	2.5×10^{9}	2.8×10^{9}	2.8×10^{9}	3.2×10^{9}
Silicic acid (moles)	3.3×10^{10}	3.5×10^{10}	4.8×10^{10}	3.2×10^{10}

[1] Park et al. (1972)

[2] Dahm (1980)

[3] This study

primary production, respiration, excretion of dissolved organic matter, and consumption. Temperature distribution in the Columbia River Estuary is a complex function of season, tidal period, day-night periods, river flow, offshore phenomena such as upwelling, and atmospheric conditions such as storms, cloud cover, rainfall, fog, or open sky (see Chapter 3). On the average, there was little spatial variation in surface temperature throughout the study area at any given time of year, except near the mouth in winter. However, there was a large temporal difference. Mean surface temperatures varied from less than 6°C to greater than 20°C throughout the year, with coldest temperatures in January-February and warmest in July-August. Vertical temperature distributions through the top 10 m were uniform in all the channels, but there was strong temperature stratification in the lower estuary in winter, with river water colder than ocean water. Strong vertical temperature gradients were also found in summer, with warmer river water at the surface overriding colder marine water at the bottom. Spring and fall were transition periods.

Metabolic rates of organisms are affected by temperature in such a way that a 10°C temperature increase will normally bring about a doubling of the rates, if the 10°C increase is within the temperature tolerance limits of the organisms (Davis and McIntire 1983). Thus, the mean temperature change from the winter low to the summer high would be expected to approximately double metabolic rates of phytoplankton and benthic microalga in the Columbia River Estuary. Phytoplankton productivity was thought to be controlled mainly by light, however, as indicated previously (and see Section 7.1.5).

Salinity

Salinity is an important ecological variable in an estuary, because it defines tolerance zones for freshwater and saltwater plants. Salinity distribution in the Columbia River Estuary is a complex function of tidal range and riverflow; variations during the tidal day are large. Upwelling and other seasonal offshore phenomena, and atmospheric conditions such as storms and rainfall, also affect salinity patterns in the Columbia River Estuary. However, it is clear that tidal and riverine effects far outweigh any atmospheric effects on salinity distribution (see Chapter 3). Because salinity distribution is so significant in determining phytoplankton, benthic algal, and vascular plant species associations and distributions in the lower estuary, a rough analysis of salinities by riverflow, tidal stage and depth is given here (Table 7.7) for the western and eastern halves of both region 1 and regions 3 + 5. The eastern boundary of regions 3 + 5 is the approximate farthest extent of measurable salinity into the estuary, under all conditions except during low riverflow and neap tides when the flood tide salinity intrusion moves into the channel bottom in regions 7 and 8. Regions 3 + 5 formed the general mixing zone in which freshwater phytoplankton began to disappear from the water column during spring and summer (Figure 7.6), and chlorophyll concentrations declined dramatically (Figure 7.9). The combined conditions of high riverflow (normally in winter and early spring) and an ebb tide can bring fresh and near-fresh water all the way to the estuary mouth (Table 7.7). Under these latter conditions, freshwater diatoms can be transported to

Table 7.7. Approximate salinity ($^{\circ}/_{\circ\circ}$) distribution in the Columbia River Estuary[1]. Regions are shown in Figure 7.1.

River flow	Tide condition	Depth (m)	Region 1		Regions 3+5	
			west	east	west	east
Low	Flood	0	30	30	30	1
"	"	5	30	30	30	5
"	"	10	30	30	30	10
Low	Ebb	0	7	3	3	0
"	"	5	10	5	5	0
"	"	10	13	8	8	0
High	Flood	0	15	5	5	0
"	"	5	30	27	27	0
"	"	10	30	30	30	0
High	Ebb	0	0	0	0	0
"	"	5	1	0	0	0
"	"	10	5	2	2	0

---

[1] After U.S. Army Corps of Engineers (1960), and Chapter 3, this report.

Table 7.8. Physical setting for the vascular plant intensive study sites. H is high marsh, L is low marsh.

Site	River Mouth Distance km	Above MLLW Elevation m	Diel Tidal range(m)	Mean Surface Salinity(°/oo)	
				High Flow	Low Flow
Baker Bay:					
China Cove/*Carex* (L)	7.4	1.83	2.44	5.0	16.8
China Cove/*Scirpus* (L)	7.4	1.86	2.44	5.0	16.8
Ilwaco (L)	7.8	1.98	2.44	5.0	16.8
Trestle Bay:					
West (L)	8.5	2.25	2.47	3.9	13.0
West (H)	8.5	2.59	2.47	3.9	13.0
East *Carex* (L)	9.5	2.19	2.50	3.3	11.5
East (L)	9.5	2.39	2.50	3.3	11.5
East (M)	9.5	2.57	2.50	3.3	11.5
East (H)					
Youngs Bay:					
Outer (L)	17.0	1.95	2.68	0.3	5.0
Inner (L)	20.0	2.06	2.65	0.1	4.0
Grays Bay:					
Outer (L)	31.2	0.88	2.47	0.0	0.5
Outer (H)	31.2	1.80	2.47	0.0	0.5
Inner (L)	31.6	2.53	2.47	0.0	0.5
Inner (H)	31.6	2.53	2.47	0.0	0.5
Cathlamet Bay:					
Army Corps Dock (L)	26.4	1.63	2.59	0.0	0.5
Lois Island (L)	28.4	1.52	2.59	0.0	0.5
Russian Island (H)	34.0	1.87	2.47	0.0	0.0
Karlson Island (L)	35.5	0.88	2.47	0.0	0.0
Tronson Island (H)	42.7	1.91	2.32	0.0	0.0
Fluvial Zone:					
Quinns Island (L)	44.2	1.33	2.32	0.0	0.0
Puget Island *Typha* (H)	60.1	2.09	2.01	0.0	0.0

the estuary mouth and beyond.

As with temperature, strong oblique salinity gradients are found during much of the year in the water column of the lower estuary (see Chapter 3). During flood tide, strong vertical gradients are often, but not always, found during the summer in the lower estuary. Riverflow and the neap-spring tidal transition are the most important phenomena that govern the maximum salinity intrusion into the estuary (see Chapter 3).

Salinities in the main body of the estuary might not be completely representative of those in the bays or in water impinging on low marsh regions. Therefore, approximate distances of the vascular plant study sites from the river mouth, elevation above MLLW, diel tidal ranges, and salinities under high and low riverflow have been extrapolated from data in Chapter 3 (Table 7.8). The tidal range is fairly consistent, between 2.4 and 2.6 m throughout the lower estuary and estuarine mixing zone to Karlson Island; but it decreases gradually into the fluvial zone. Nearly fresh water is found at the Youngs Bay sites during high riverflow, a condition brought about not only by high Columbia River flow, but also by high flow from the Youngs and Lewis and Clark Rivers. During low flow of the Columbia and tributary rivers, brackish water is found at the Youngs Bay sites. Salinity excursions of about 10°/₀₀ are found at the Baker Bay and Trestle Bay sites, depending on the river flow. Fresh water is rarely observed in Baker Bay and Trestle Bay.

Sediment Properties

The properties and stability of the sediment are closely related to species composition and production dynamics of benthic plant assemblages in the Columbia River Estuary. Sedimentary environments and transport are considered in detail in Chapter 4; however, specific sediment samples were also collected for grain-size analysis from the five intensive study sites where benthic primary production was measured (Figure 7.3). The results of this analysis (Table 7.9) are summarized for comparison with corresponding data for microalgal biomass (Table 7.4), and for later comparison with benthic primary production. The sediments along the upper, mid and lower sampling transects at Clatsop Spit were well sorted (low sorting measure, Table 7.9), and consisted of fine sand. Moreover, it was obvious from field observations that the sediments at this site shifted in response to river flow and tidal movement, and in general were an unstable substrate for the growth of aquatic plants. At the Youngs Bay and Baker Bay sites, the sediments were relatively fine, and in comparison with samples from Clatsop Spit, these sediments were poorly sorted. Sediments at the intensive study site in Grays Bay were composed of sandy silt, whereas the intertidal region at the intensive study site on Quinns Island was a sandy area with relatively little silt and clay.

The productive capacity of the tidal flats of the Columbia River Estuary apparently is closely related to the degree to which the sediments are disturbed by physical processes. Unfortunately, there is no reliable, direct measure of sediment mixing or disturbance. However, in the intertidal zones where diatoms are the dominant autotrophic organisms, the ratio of the chlorophyll a concentration near the

Table 7.9. Summary of sediment grain size analysis for five intensive study sites. Transects and sites are the same as those indicated in Table 7.4. Mean grain size is expressed in phi units, while measurements of sorting and skewness are dimensionless (Inman, 1952). The values are the means of n observations.

Site	n	% Sand	% Silt	% Clay	phi	Sort	Skew
Clatsop Spit:							
Upper	8	00.7	0.3	0.1	2.47	0.25	0.04
Mid	1	00.4	0.6	0.0	2.37	0.32	0.23
Lower	8	99.6	0.4	0.1	2.36	0.30	-0.07
Youngs Bay:							
Upper	8	9.2	78.3	12.5	5.84	1.65	0.35
Mid	1	27.1	63.1	9.8	4.70	1.76	0.19
Lower	8	56.2	36.4	7.3	4.34	2.08	0.51
Baker Bay:							
Upper	8	57.5	31.9	10.7	4.61	1.89	0.46
Mid	1	72.3	21.2	6.4	3.73	0.62	0.30
Lower	8	30.5	55.0	14.6	5.69	2.10	0.38
Grays Bay:							
Upper	8	69.4	26.8	3.9	4.29	1.31	0.60
Mid	1	86.4	10.6	3.0	3.26	0.74	-0.04
Lower	8	43.0	51.7	5.4	4.69	1.25	0.37
Quinns Island:							
Upper	8	92.5	6.4	1.2	2.21	1.11	0.33
Mid	1	97.2	2.8	0.0	1.63		
Lower	8	81.2	15.6	3.2	2.78	1.02	0.81

sediment surface to that at other depths below the surface provided a crude biological index to sediment mixing. Mobile, epipelic diatoms tend to remain in the upper few millimeters of sediment where the light intensity is sufficient for photosynthesis, but many species can survive burial for long periods of time by switching to a heterotrophic mode of nutrition. Consequently, chlorophyll in living diatoms can serve as an indicator of the vertical mixing which results from water movements or the activities of burrowing animals. In the Columbia River Estuary, the ratios of the chlorophyll a concentration in the top cm of sediment to that at the 4.5 - 5.5 cm depth (C1:C2) and to that at the 9-10 cm depth (C1:C3) were used to estimate vertical mixing of sediments (Table 7.10). Ratios near 1 indicated well-mixed sediments, while ratios greater than 1 indicated the degree of stabilization (the larger the numerical value of the ratio, the greater the lack of mixing or degree of stabilization).

Sediment disturbance was less pronounced at the sites in Youngs Bay and Baker Bay than at the sites in Grays Bay and on Quinns Island (Table 7.10). In particular, sediment disturbance in Grays Bay was relatively high, as the mean ratios for this location were 0.93 and 1.81. This likely was an effect of wind waves (Jay, personal communication). The ratios for the site on Quinns Island also were relatively low, but with more seasonal variation (not shown) than the ratios calculated for the site in Grays Bay. The C1:C3 ratios for Youngs Bay and Baker Bay indicated that mixing was greater in the lower intertidal areas than in the upper intertidal areas in the vicinity of the low marsh. Moreover, these sites and transects with high chlorophyll ratios (low sediment mixing) corresponded to regions in the estuary with relatively high rates of benthic primary production (see Section 7.1.5).

7.1.5 Primary Productivity

Primary productivity is the rate at which light energy and nutrients are incorporated into phytoplankton, benthic algae and vascular plants to produce more plant biomass (Fig. 7.2). Temperature and other physical variables act to control primary productivity, and there are several process-generated and non-process-generated losses.

Phytoplankton

The vertical distribution of primary productivity, as net carbon incorporated (mgC m^{-3} hr^{-1}) by the phytoplankton community at three representative stations along the main navigation channel of the Columbia River Estuary, is shown in Figure 7.14. A clear seasonal cycle was evident, with maximum summer rates up to 35 mgC m^{-3} hr^{-1} near the surface and minimum near-surface values during November (2-5 mgC m^{-3} hr^{-1}). No data were available for December or January, but productivity during these months was probably lower than or equal to November productivity, due to low daily solar irradiation and a shallow photic depth. The depth of zero or near-zero net productivity was about 1m in November but 3-4 meters in July, coinciding with the photic depths for those months. With few exceptions, primary productivity was not light-saturated at any depth in the water column from September to February (Figure 7.14); that is, maximum productivity values were almost

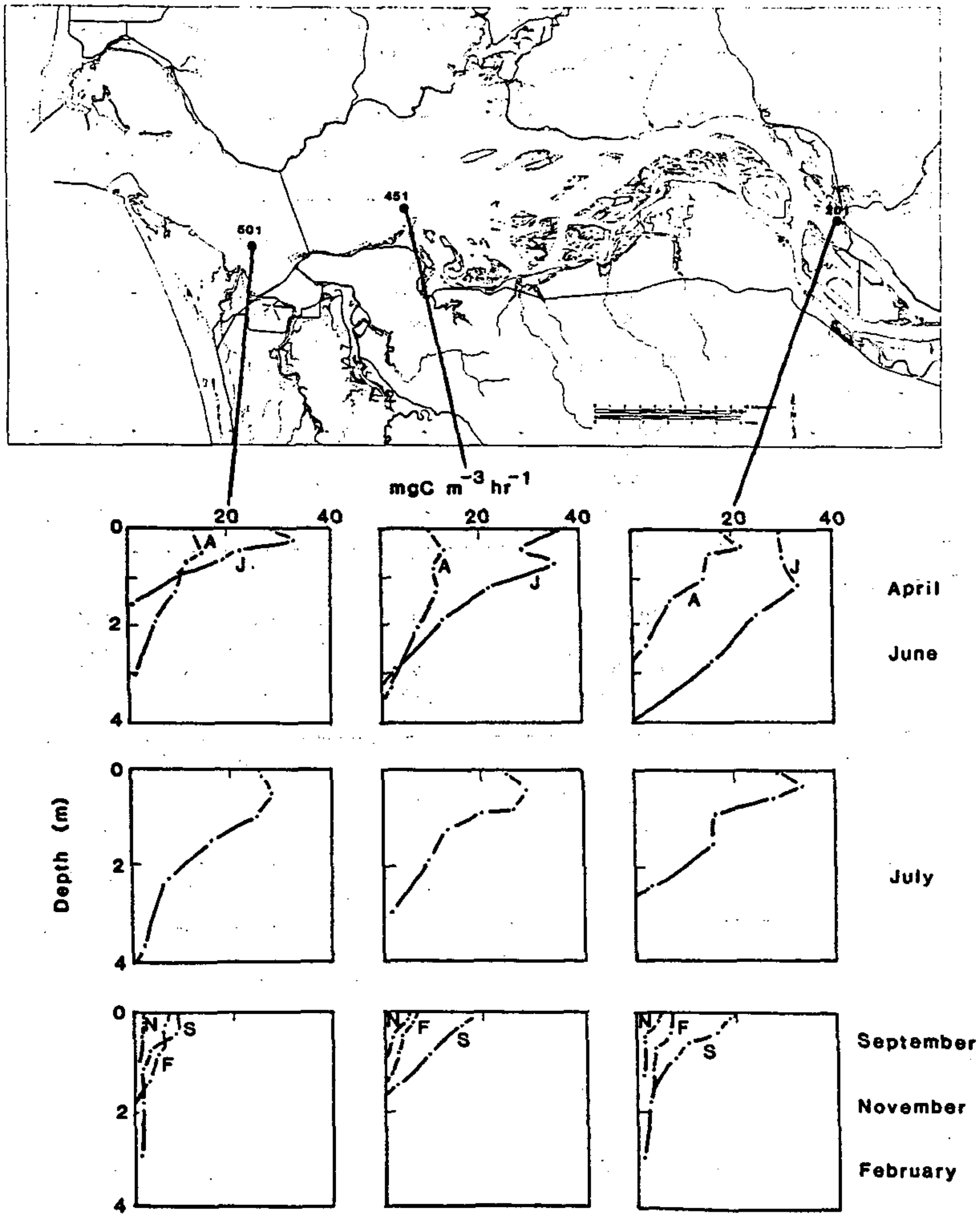


Figure 7.14. Vertical distribution of primary production in the water column (mgC m^{-3} hr^{-1}) at three sampling stations in the navigation channel.

Table 7.10 Ratios of the concentration of chlorophyll a in the top cm of sediment to the concentrations at the 4.5-5.5 cm depth (C1:C2) and at the 9-10 cm depth (C1:C3) at four intensive study sites. Data are mean values for n observations at the same transects described in Table 7.4.

Site	Transect	n	C1:C2	C1:C3
Youngs Bay:				
	Upper	72	4.00	10.06
	Mid	66	3.61	5.96
	Lower	66	4.48	5.11
	Mean	204	4.03	7.13
Baker Bay:				
	Upper	72	3.64	11.00
	Mid	66	3.30	10.21
	Lower	66	3.69	5.42
	Mean	204	3.55	9.05
Grays Bay:				
	Upper	66	0.91	1.47
	Mid	66	0.86	1.50
	Lower	60	1.02	2.54
	Mean	192	0.93	1.81
Quinns Island:				
	Upper	72	2.59	2.93
	Mid	66	1.68	2.72
	Lower	60	2.42	3.06
	Mean	198	2.26	2.91

never found at some depth below the water surface from September to February. During May 1980, suspended material resulting from the eruption of Mount St. Helens caused a marked reduction in the photic zone depth and hence in the primary production rates (not shown in Figure 7.14).

Net carbon fixed by the phytoplankton community in selected shallow areas of the estuary exhibited a seasonal trend similar to the channel stations (Figure 7.15), with maximum values during summer (25-45 mgC m^{-3} hr^{-1}) and minimum values during November (1.5-3.0 mgC m^{-3} hr^{-1}). Primary productivity of small tributaries sometimes reached 80 mgC m^{-3} hr^{-1} in summer (not illustrated).

Phytoplankton net productivity in units of mgC m^{-3} hr^{-1} was integrated over depth and the daylight portion of each day to yield daily production beneath a square meter of estuary surface (mgC m^{-2} day^{-1}). This was done in order to compare spatial and temporal variability of productivity, and to examine light, nutrient, temperature and other effects on that productivity. Unfortunately there were no measurements of phytoplankton night respiration which, if available, would have been subtracted from net daytime primary production to yield net 24-hr production. An average 29% respiratory loss, derived from benthic algal data, was used to estimate net 24-hr phytoplankton production in Chapter 8.

Regression models which related net primary productivity, on a "daylight day" basis, to ten environmental variables were developed for both deep-water and shallow-water areas. Multiple regression analysis was done by a "forward stepwise" procedure which selected the variables that were most closely associated with primary productivity (Rowe and Brenne 1981). The best linear models obtained from this analysis are shown in Tables 7.11 and 7.12. In the model for deep-water stations (Table 7.11), daily surface solar radiation accounted for 58% of the variability in daily primary productivity, and the light attenuation coefficient (k) accounted for an additional 17% of the variability. Therefore, these two variables together accounted for 75% of the variability, which supported the hypothesis that light availability exerted the primary control on daily phytoplankton productivity. Chlorophyll a concentration, water temperature, and total seston concentration together accounted for 15% more of the variability. All five factors combined accounted for 90% of the variability in daily primary productivity in deep waters throughout the year. Concentrations of dissolved phosphate, nitrate+nitrite, silicate, organic suspended particles, and phaeophytin a did not contribute significantly to the model. The insignificant effect of nutrient concentrations was in accord with the notion that nutrient supply exerted little control over daily phytoplankton productivity in the Columbia River Estuary. In the regression model for shallow-water stations, daily surface solar radiation, chlorophyll a concentration, and k accounted for 85% of the variability in productivity (Table 7.12), while the other seven variables did not contribute significantly.

Both measured and model-predicted values for phytoplankton productivity at the deep-water stations showed strong seasonal variation

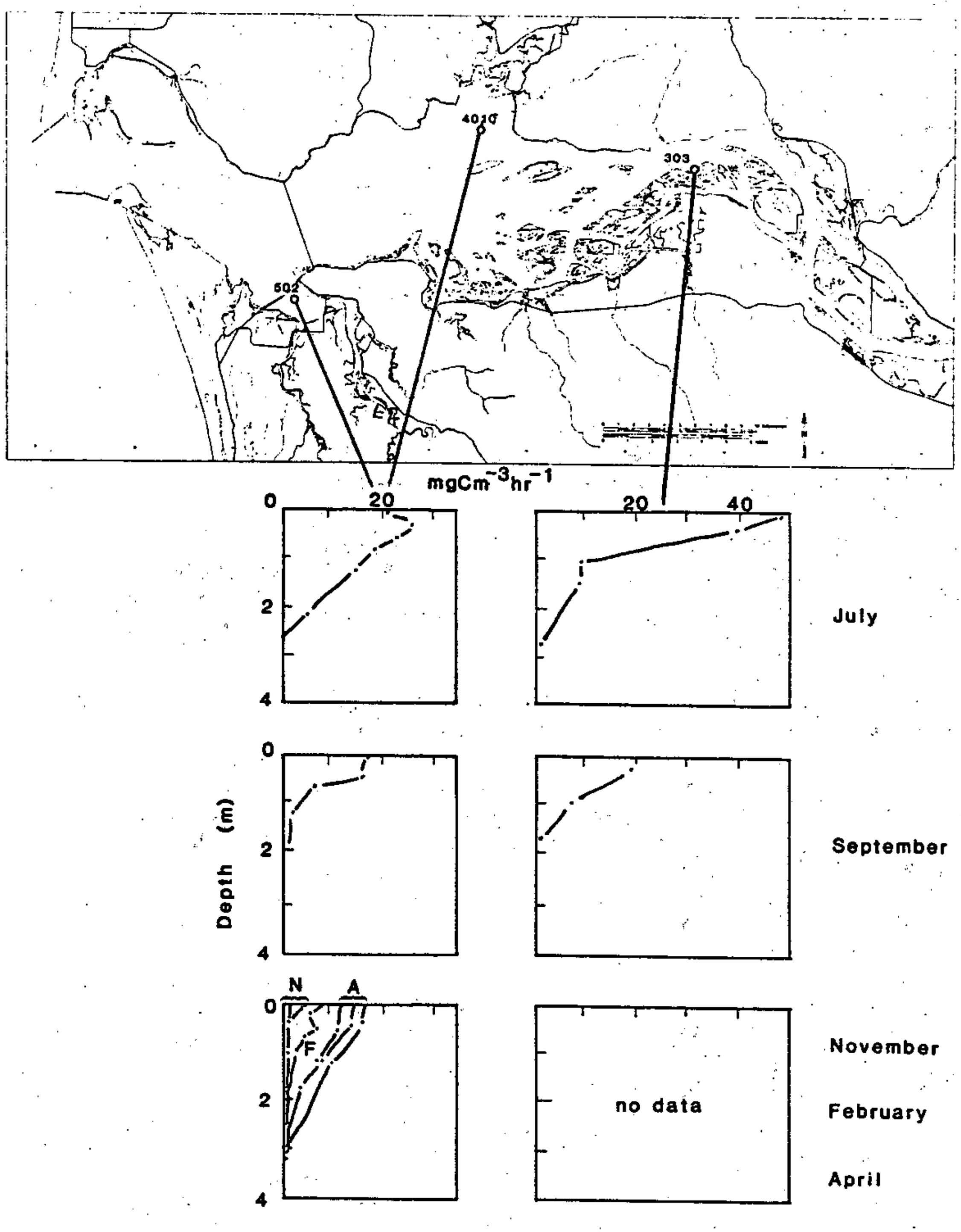


Figure 7.15. Vertical distribution of primary production in the water column (mgC m^{-3} hr^{-1}) at three sampling stations in shallow-water areas.

Table 7.11. Primary productivity (mg C m^{-2} day^{-1}) regression model for deep water stations in the main body of the study area, mainly over channels (n=29). R^2 = coefficient of determination. See text for further details.

VARIABLE	cumulative R^2
LITE = Daily solar radiation (g cal cm^{-2} day^{-1})	0.58
k = Light attenuation coefficient (m^{-1})	0.75
CHLOR = Chlorophyll a (mg m^{-3})	0.84
TEMP = Temperature (°C)	0.87
TSP - Total seston (mg l^{-1})	0.90

MODEL

Log daily productivity = 1.548 + 0.001 LITE - 0.103 k + 0.056 CHLOR + 0.028 TEMP - 0.001 TSP

Table 7.12. Primary productivity (mgC m^{-2} day $^{-1}$) regression model for peripheral bays and shallows (n=28). R^2 = coefficient of determination. See text for further details.

VARIABLE	cumulative R^2
LITE = Daily solar radiation (g cal cm^{-2} day $^{-1}$)	0.73
CHLORO = Chlorophyll *a* (mg m^{-3})	0.78
k = Light attenuation coefficient (m^{-1})	0.85
MODEL	

Log daily productivity = 1.605 + 0.003 LITE + 0.033 CHLOR - 0.127 *k*

(Figure 7.16). Values during summer averaged 795 mgC m^{-2} day^{-1} (range 467-1448 mgC m^{-2} day^{-1}), and productivity in November averaged 64 mgC m^{-2} day^{-1} (range 19-102 mgC m^{-2} day^{-1}). The eruption of Mount St. Helens markedly reduced the daily photosynthetic rates in May 1980 by dramatically increasing the light attenuation in the water column. A potential production rate for May, without the effects of the volcano, was estimated by using the regression model in Table 7.11. Substituting k and total seston values obtained by averaging values for April and July, and using the actual chlorophyll a, temperature, and incident light values measured in May, a potential production rate of 660 mgC m^{-2} day^{-1} was obtained from the model. Actual measured production values in May averaged 115 mgC m^{-2} day^{-1} (range 22-214 mgC m^{-2} day^{-1}). The difference between the measured rate of carbon uptake and the calculated rate represented an average reduction in daily water-column primary production of 82%.

At shallow-water stations in three peripheral bays, phytoplankton productivity showed the same seasonal trends as in the deep-water stations (Figure 7.17). Summer (July) productivities averaged 767 mgC m^{-2} day^{-1} (range 421-1026 mgC m^{-2} day^{-1}), and late fall (November) rates averaged 28 mgC m^{-2} day^{-1} (range 17-50 mgC m^{-2} day^{-1}), not significantly different (p greater than 0.05) from mean rates in the deep-water stations. Similarity of productivity in shallow and deep stations further suggested light control; i.e., shallow photic depths made "shallow-water stations" out of all sampling stations.

Phytoplankton productivity (mgC m^{-3} hr^{-1}) at surface light intensity for the three cell-size fractions analyzed for biomass (Figure 7.11) is shown in Figure 7.18. Highest rates of production were associated with cells either larger than 33 um or smaller than 10 um at all times of year. The less-than-10 um fraction had the highest photosynthetic rates in winter, and rates for both the less-than-10 um and greater-than-33 um fractions increased most dramatically in spring and summer. During the period from April through July, the greater-than-33 um fraction (mainly diatoms) accounted for 50% of the total production. The productivity pattern by size fraction corresponded closely to the chlorophyll pattern by size fraction (Figure 7.11), particularly for Station 501.

Estimates of mean daily net primary productivity on a per daylight-day basis (mgC m^{-2} day^{-1}) for each sampling month for regions 1, 3 + 5, 7 and 8 are given in Figure 7.19. The Fluvial and Cathlamet Bay Regions were the most productive in summer, but through the rest of the year primary productivity in all the regions was remarkably similar. The decrease in chlorophyll a content from the Fluvial Region to the Entrance Region observed every month of sampling (Figure 7.9), was observed in the productivity data only in May and July 1980. This suggested that for much of the year the production efficiency (production per unit of chlorophyll) was actually greater in regions 1 and 3 + 5 than in regions 7 and 8. The spatial-temporal distribution of assimilation number [mgC $(mgChla)^{-1}$ hr^{-1} at light saturation] neither supported nor refuted the suggestion (Frey et al, 1984). Comparison of assimilation numbers with production efficiencies based on depth-integrated productivity and chlorophyll values might not be valid for

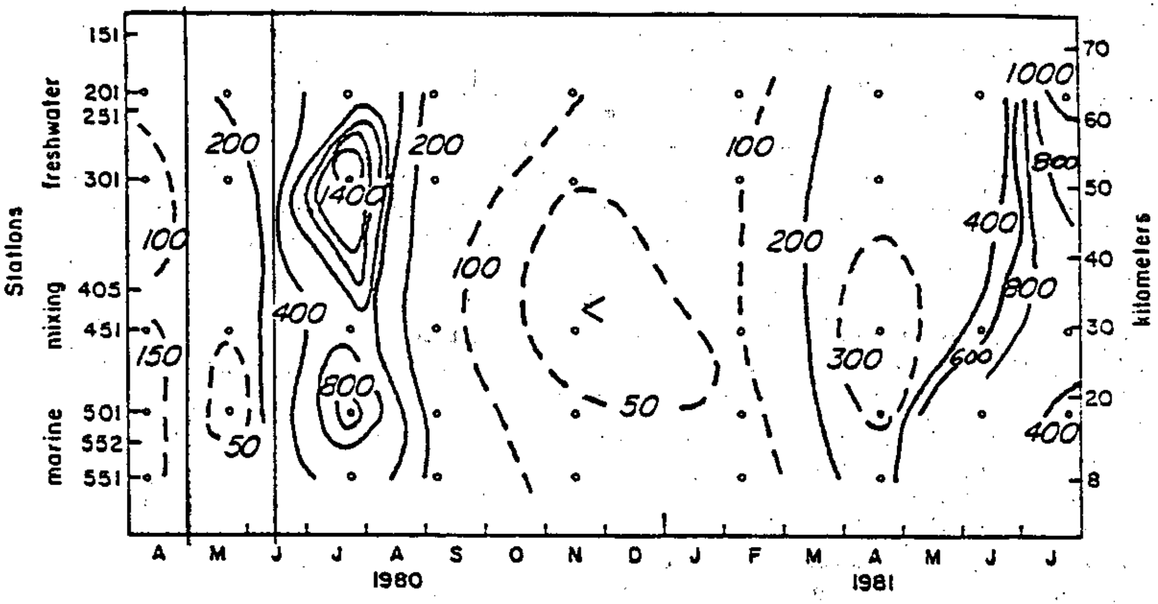


Figure 7.16. Spatial-temporal distribution of primary productivity in the water column (mgC m^{-2}day^{-1}) in the deep-water regions of the study area. Dashed lines represent a contouring interval different from that represented by solid lines. The two vertical lines separating May and half of June 1980 from the other months isolate the time period over which Mt. St. Helens volcanic debris was evident in the water column.

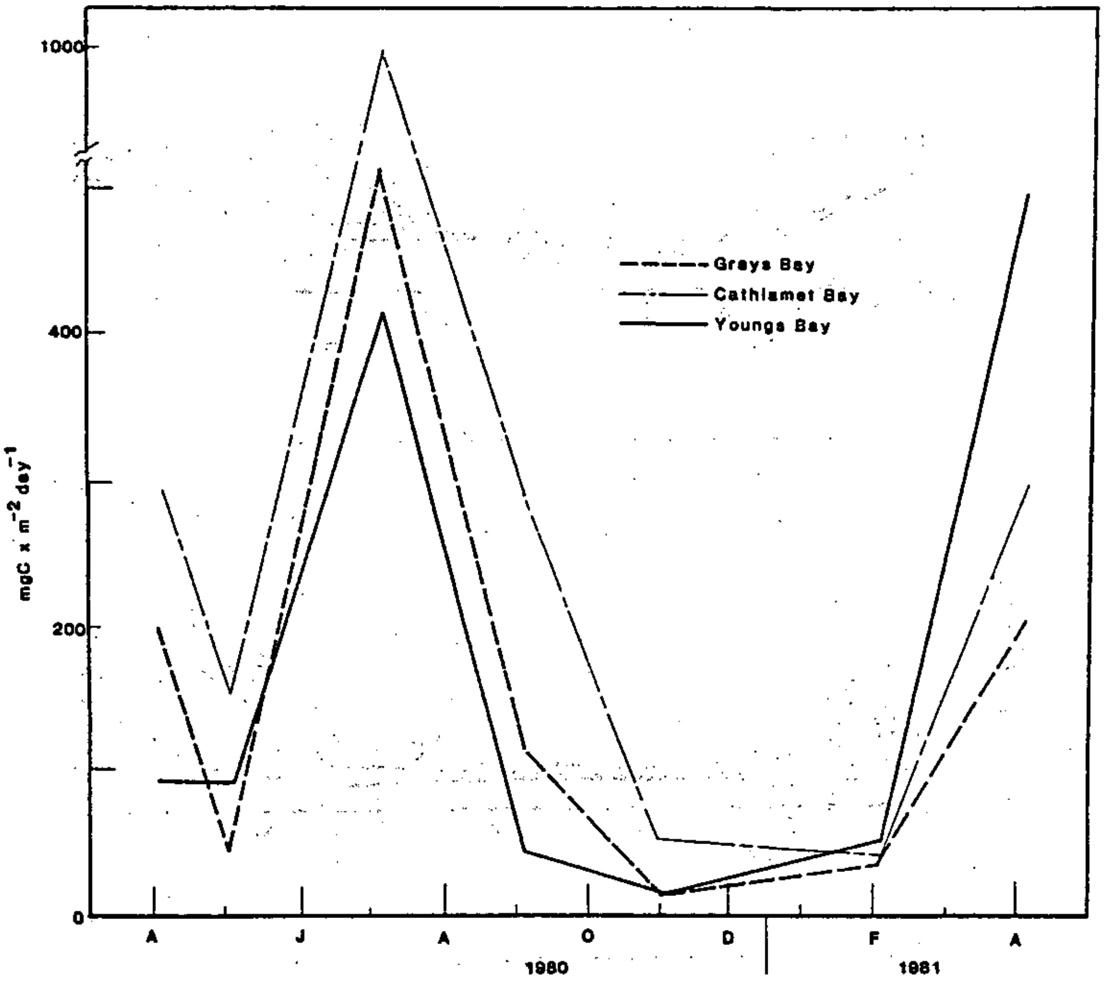


Figure 7.17. Primary productivity in the water column (mgC $m^{-2}day^{-1}$) in selected shallow-water areas.

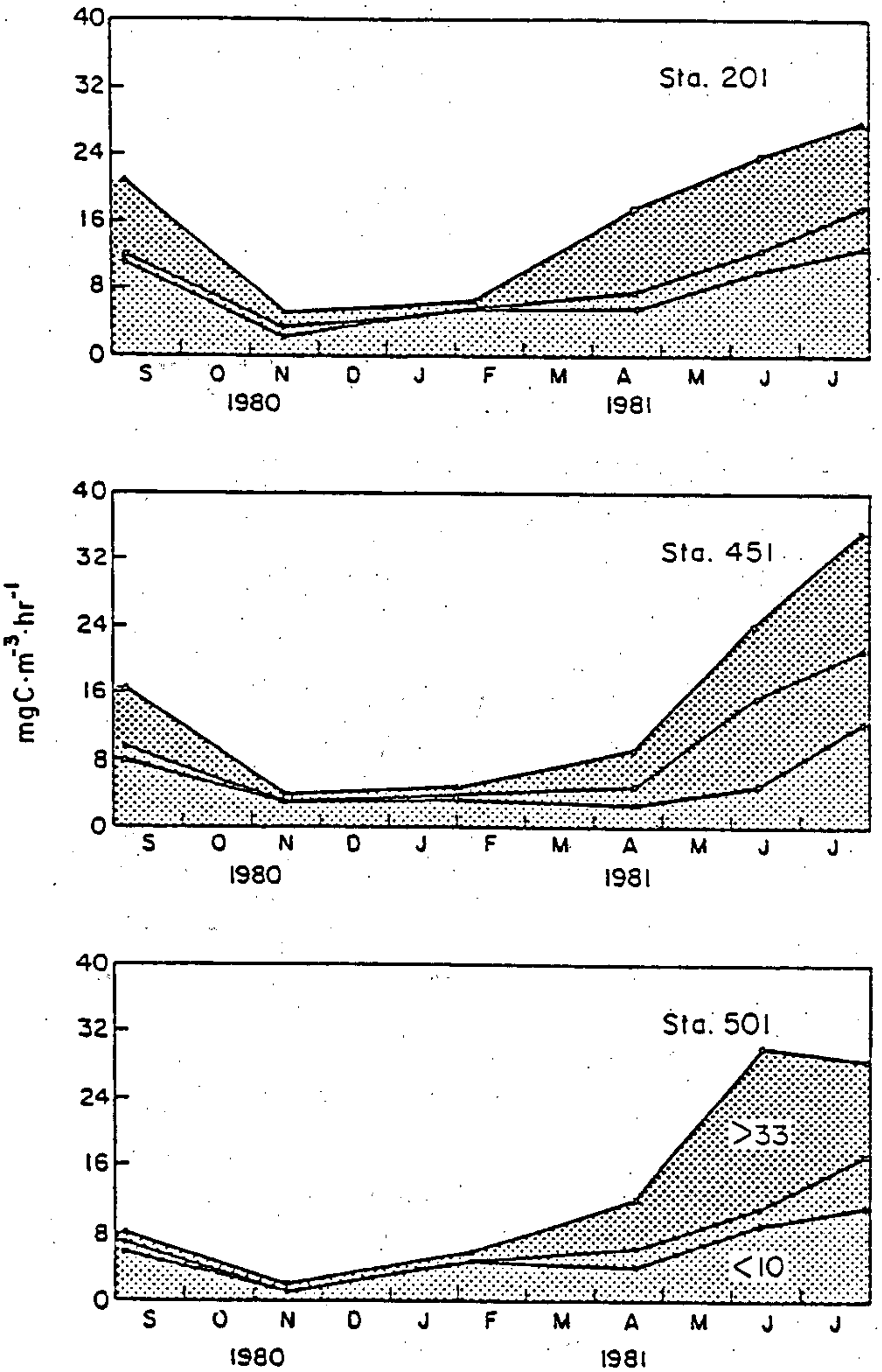


Figure 7.18. Primary productivity (mgC m^{-3} hr^{-1}) of three size fractions of phytoplankton (>33 µm, 10-33 µm, and 10 µm) at three stations along the main navigation channel of the estuary.

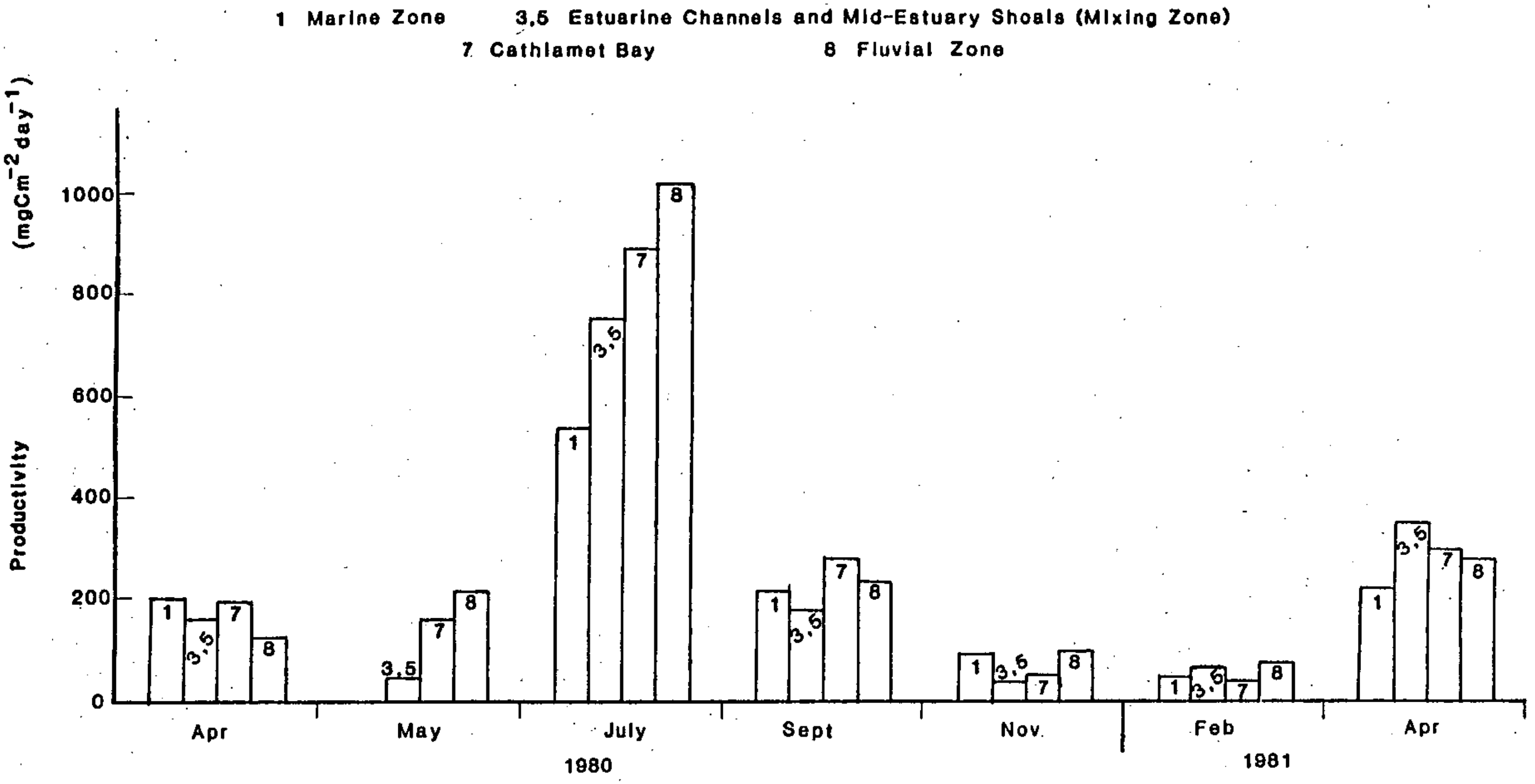


Figure 7.19. Mean daily phytoplankton productivity (mgC m^{-2} day^{-1}) by sampling months and regions along the main axis of the Columbia River Estuary. May 1980 concentrations are reduced because of the Mt. St. Helens eruption.

the Columbia River Estuary, however.

Seasonal productivity patterns for selected shallow bays and tributary rivers (Figure 7.20) showed that the small rivers (Regions 9 and 10) were the most productive regions, on a per unit area basis, from May through September. However, because of their small area, these small rivers did not significantly affect productivity estimates for the main body of the estuary. The productive Youngs River and Lewis and Clark River both discharge into the relatively unproductive Youngs Bay, and Deep River, which is productive in September, discharges into the relatively unproductive Grays Bay. In May 1980, the effect of the volcanic eruption apparently had not yet reached into either the Youngs River or the Lewis and Clark River, as their combined productivity was very high relative to Youngs Bay (Figure 7.20) and to the main body of the estuary (Figure 7.19). The May 1980 productivity of the Youngs River and Lewis and Clark River likely represented the normal productivity condition for May in these systems.

Benthic Algae

Benthic primary productivity measurements were analyzed in relation to concurrent measurements of microalgal biomass, community oxygen uptake, the concentration of organic matter in the sediment, and selected physical variables. Therefore, these data provided a basis for exploring relationships among selected biological rate and state variables, and between these variables and selected physical variables.

Mean rates of gross primary production for all intensive study sites ranged from 11.1 mgC m^{-2} hr^{-1} in February 1981, to 75.7 mgC m^{-2} hr^{-1} in May 1980 (Table 7.13). In general, rates were lower in the winter than at other times of the year. Youngs Bay was the most productive site, Clatsop Spit was the least productive, and the other sites were intermediate. Water-column net primary productivity was about equal in Youngs Bay and Grays Bay over most of the year (Figure 7.20), unlike the benthic algal gross productivities at the two sites. Patterns of mean benthic primary productivity at the intensive study sites were similar to patterns of the mean chlorophyll a distribution at those sites (Table 7.4), with the exception that mean primary productivity at Baker Bay was lower than would be expected from its mean concentration of chlorophyll a. The mean rate of gross primary production was higher for cores obtained from the marsh and upper intertidal transects than for cores sampled from the lower intertidal transects (Table 7.13), a pattern similar to the corresponding pattern of chlorophyll a (Table 7.4).

Correlation coefficients relating the rate of gross benthic primary production to oxygen uptake by the sediments and to the chlorophyll a concentration in the top cm of sediment were relatively high for the intertidal transects (Table 7.14). In particular, the high value ($r = 0.81$) for gross primary productivity and chlorophyll a concentration (CHLOR) indicated that the latter variable could be used for the prediction of benthic primary productivity in regions where direct measurements were not available. Benthic primary productivity had a lower correlation with organic matter concentration in the top cm of

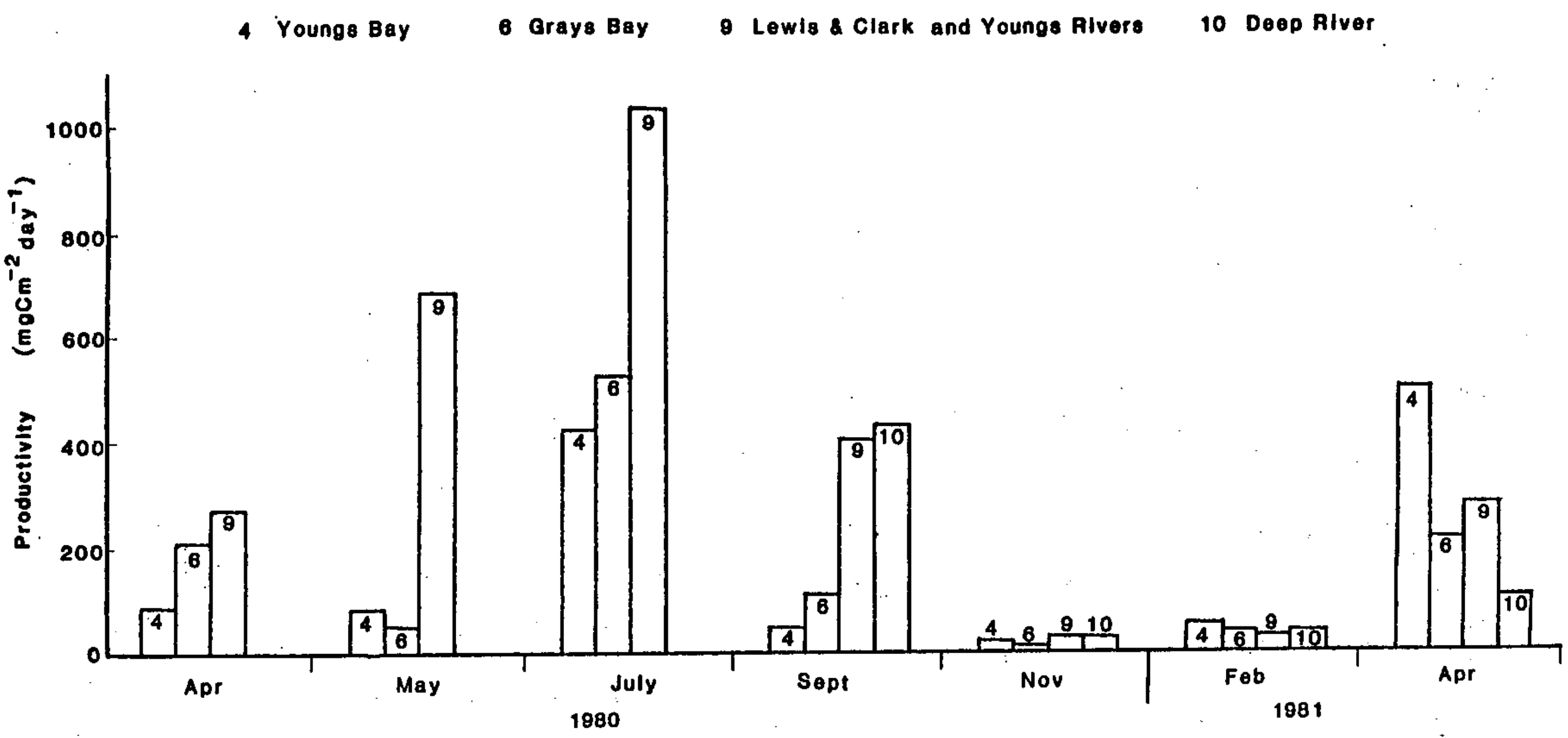


Figure 7.20. Mean daily phytoplankton productivity (mgC m^{-2} day^{-1}) by sampling months and regions in shallow-water bays and tributaries of the Columbia River Estuary.

Table 7.13. Mean rates of gross primary production (mgC m^{-2} hr^{-1}), sample size, and standard errors of means for five intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site, and tidal level (transect).

Variable	Sample Size	Mean	Standard Error
Time:			
May	14	75.7	28.7
June	14	39.1	9.3
July	12	51.6	10.8
August	14	37.5	6.4
September	14	48.1	13.4
October	14	53.4	12.8
November	7	28.4	8.1
February	14	11.1	4.4
March	14	38.9	7.5
April	14	31.5	7.4
Site:			
Clatsop Spit	17	5.2	1.9
Youngs Bay	29	84.2	14.4
Baker Bay	29	42.5	5.2
Grays Bay	29	33.0	4.9
Quinns Island	29	29.6	5.6
Tidal Level Transect:			
Marsh (0.9m above MLLW)	39	55.0	10.9
Upper (0.7m above MLLW)	48	43.2	6.0
Lower (0.3m above MLLW)	44	29.4	4.7

Table 7.14. Pearson product-moment coefficients of correlation (r) relating the rate of gross benthic primary production (GPP) to selected biological and physical variables monitored along the intertidal transects (not including the marsh transect) at the intensive study sites from May 1980 to April 1981. Biological variables are benthic oxygen uptake (OCON), chlorophyll a concentration of organic matter in the top cm of sediment (CHLOR), and concentration of organic matter in the top cm of sediment (AFDW). Varables related to sediment properties are mean grain size in phi units (MEAN), the sorting coefficient (SORT), the skewness coefficient (SKEW), and the chlorophyll ratios (Cl:C2 and Cl:C3). Other physical variables are surface light intensity (LITE), temperature (TEMP), and salinity (SALT), during the respirometer measurements.

Variable	Number of Sample Pairs	r	Significance ($p = 0.05$)
Biological:			
OCON	90	0.81	yes
CHLOR	90	0.81	yes
AFDW	90	0.54	yes
Physical:			
MEAN	77	0.44	yes
SORT	77	0.42	yes
SKEW	77	-0.02	no
Cl:C2	72	0.56	yes
Cl:C3	72	0.68	yes
LITE	92	-0.15	no
TEMP	92	0.30	yes
SALT	92	0.11	no

sediment (r = 0.54) than with the corresponding concentration of chlorophyll a, a pattern presumably related to detrital inputs from the marsh and water column. However, the concentration of organic matter was not as highly correlated with the rate of oxygen uptake by the sediments (r = 0.49) as with the concentration of chlorophyll a (r = 0.72) (not illustrated in Table 7.14), indicating that community metabolism on the tidal flats of the estuary might be more closely associated with autochthonous production by the microalgae than with allochthonous inputs of detritus.

For the marsh transects, detrital inputs from the stands of vascular plants were high during summer and fall, and the above-ground biomass shaded the sediment below during the growing season (about May through September). Such effects apparently caused relatively low correlations among benthic algal productivity and other biological variables. For example, the correlation (r = 0.57) between gross microalgal productivity and oxygen uptake by the sediment at the marsh transects (not illustrated) was not as high as that found for the intertidal transects (r = 0.81, Table 7.14), suggesting that some of the oxygen uptake in the marsh benthos was related to the decomposition of vascular plant material and unrelated to rates of microalgal production. The low correlation (r = 0.27) between microalgal productivity and the concentration of chlorophyll a in the marsh (not illustrated) might have been related to seasonal changes in light intensity which corresponded to the shading of the sediment surface by the vascular plants. The statistically significant, but relatively weak, correlations between the concentration of phaeo-pigments and the concentrations of chlorophyll a (r = 0.37) and organic matter (r = 0.48) probably reflected the degradation of chlorophyll a and the concurrent accumulation of detrital materials in the marsh.

In the intertidal regions of the estuary (not including the marsh transects), gross benthic primary productivity was more highly correlated with certain sediment properties than with light intensity, temperature and salinity (Table 7.14). The low correlation with light intensity in this unshaded environment was not surprising, as the benthic diatom flora reaches its maximum photosynthetic rate at light intensities about 10% of full sunlight, i.e., at about 250 uE m^{-2} sec^{-1} (Davis and McIntire, 1983). While salinity affects the species composition of the benthic diatom flora, this variable had no apparent effect on rates of benthic primary production along the intertidal transects. The microalgal flora simply adjusted its species composition to the local pattern of salinity, without a related effect on the productive capacity of the system. The correlations between benthic primary productivity and the chlorophyll ratios at different sediment depths (C1:C2 and C1:C3) were higher than between benthic primary productivity and the other sediment properties, suggesting that productive capacity may be more closely related to sediment mixing than to distribution of sediment grain size. In general, the highest rates of benthic primary production and the highest concentrations of plant pigments and organic matter were associated with sediments with a relatively small mean grain size. However, there were exceptions to this generalization, particularly at the intensive study site in Grays Bay.

Regression equations expressing the hourly rate of gross benthic primary production at light saturation in the intertidal regions, as a function of different sets of variables, are summarized in Table 7.15. Although a large number of models were examined, in most cases simple linear relationships were satisfactory for estimation of productivity in locations where direct productivity measurements were not possible. In particular, the relationship between the rate of gross primary production (GPP) and the concentration of chlorophyll a (CHLOR), and that between GPP and the concentrations of chlorophyll a and phaeo-pigments, provided valuable approaches for the expansion of estimates of benthic primary productivity from the intensive study sites to the survey sites, where concentrations of chlorophyll a and phaeo-pigments were the only available data. If the GPP-CHLOR curve is forced through the origin, model 1 in Table 7.15 becomes

$$GPP = 0.28CHLOR,$$

which suggests a GPP-CHLOR ratio of about 0.28. This ratio is fairly typical for sediment-associated microalgae, but is lower by an order of magnitude than ratios typical for phytoplankton in the photic zone.

The relationship between gross benthic primary productivity and mean grain size was relatively weak, with an R^2 value of only 0.27 (model 5, Table 7.15). The addition of the sorting and skewness coefficients to the regression model increased the R^2 value only to 0.31 (model 6). Furthermore, variability around the regression line became greater with decreasing grain size (increasing phi value), indicating that sites with fine sediment were both productive and unproductive depending on location and season. Seasonal differences in the degree of sediment disturbance among the sampling transects apparently accounted, in part, for the weak relationship between benthic primary productivity and mean grain size. However, while the chlorophyll ratio C1:C3, an index to "deep" sediment mixing, was a better predictor of benthic primary productivity than the C1:C2 ratio or mean grain size (Table 7.15), this ratio was not as good for predicting primary productivity as the chlorophyll a concentration near the sediment surface.

Rates of gross benthic primary production at 31 survey sites (Figure 7.4) were predicted using model 1, Table 7.15. Chlorophyll a concentration in the top centimeter of sediment was the only variable consistently measured at all survey sites (McIntire and Amspoker, 1984); hence, model 1 became the model of choice). At some of the sites chlorophyll a samples were obtained along transects at more than one tidal height. The regression equation generated 112 predicted values from the chlorophyll measurements, and these predictions were used along with 131 measured values at the intensive study sites and validation sites to map the distribution of benthic primary productivity over the entire study area.

Because benthic primary productivity was largely confined to the shallow regions of the estuary, most of the interesting patterns occurred in the four bays: Baker Bay, Youngs Bay, Cathlamet Bay, and Grays Bay (Figures 7.21, 7.22, 7.23, 7.24). In Baker Bay and Youngs Bay there are tidal flats that supported relatively high mean rates of

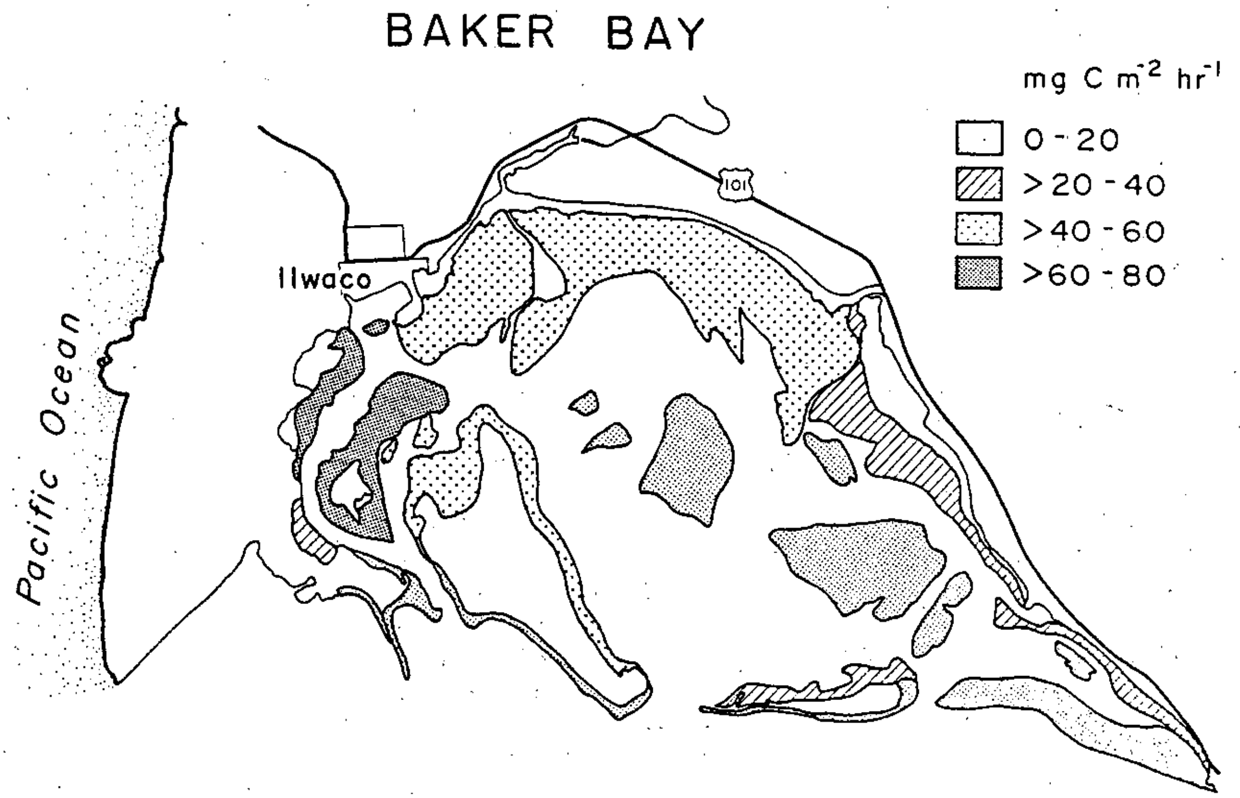


Figure 7.21. Pattern of gross primary productivity in Baker Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

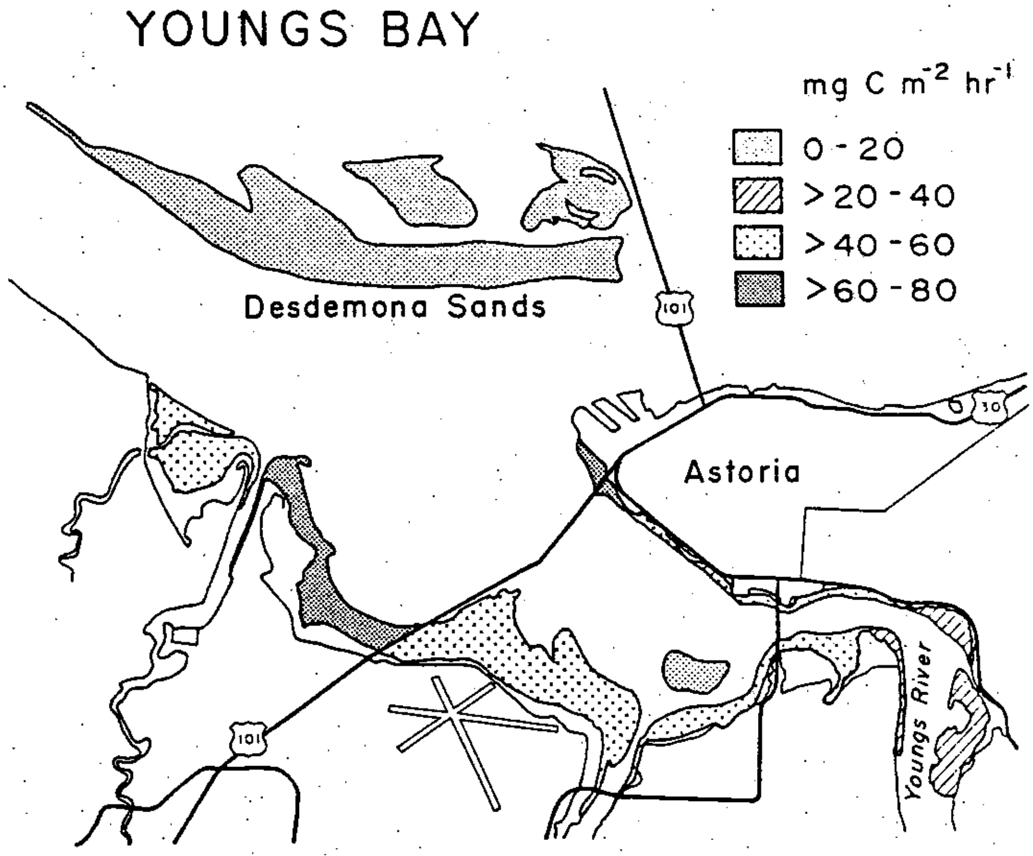


Figure 7.22. Pattern of gross primary productivity in Youngs Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

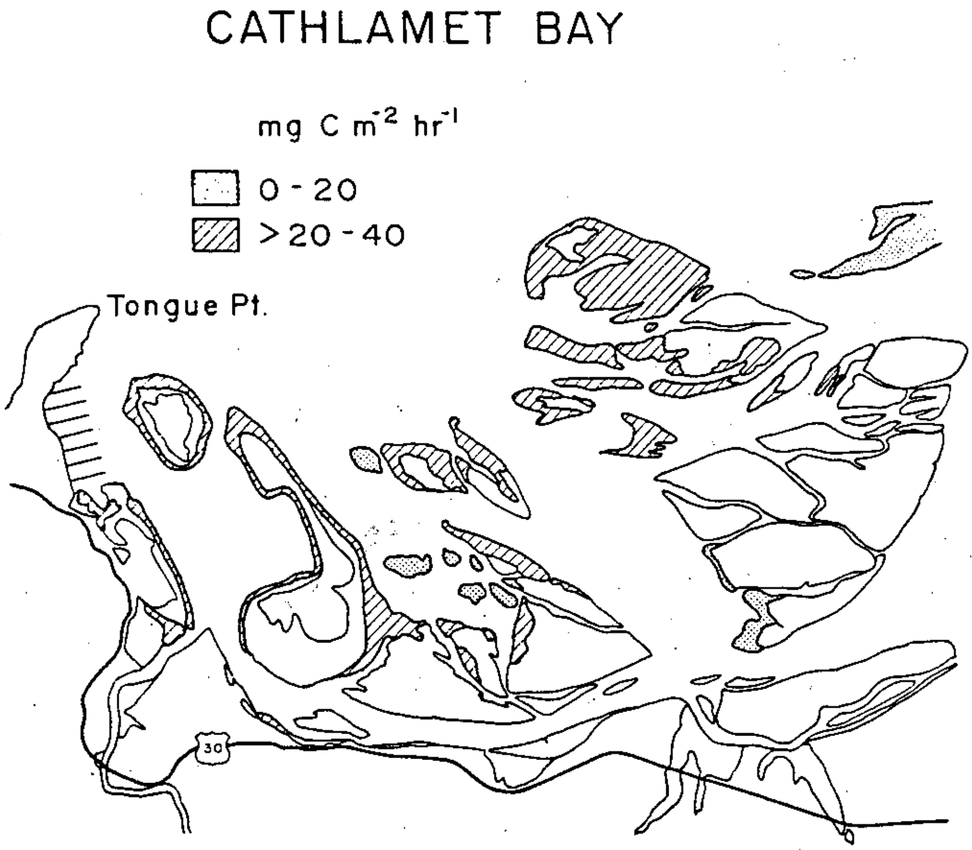


Figure 7.23. Pattern of gross primary productivity in Cathlamet Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 though April 1981.

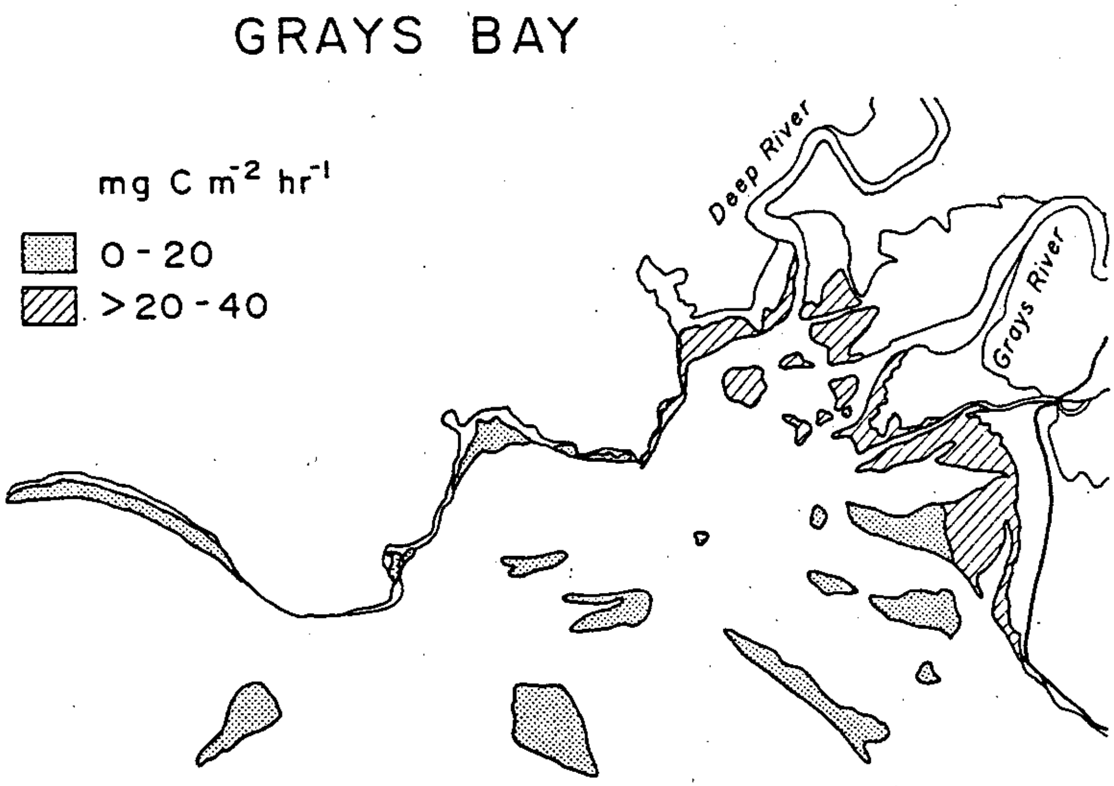


Figure 7.24. Pattern of gross primary productivity in Grays Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

Table 7.15. Linear regression equations expressing gross benthic primary productivity at light saturation (GPP) as a function of selected biological and physical variables. Other variables are the chlorophyll ratios (C1:C2 and C1:C3), mean grain size in phi units (MEAN), the sorting (SORT) and skewness (SKEW) coefficient, and concentrations of chlorophyll *a* (CHLOR) and phaeo-pigments (PHAEO) in the top cm of sediment. The unit for GPP is mgC m^{-2} hr^{-1}, and units for CHLOR and PHAEO are mg m^{-2}.

		Sample Size	R^2
1.	GPP = 0.63 + 0.28 CHLOR	90	0.66
2.	GPP = -1.38 + 0.20 CHLOR + 0.14 PHAEO	90	0.70
3.	GPP = 13.00 + 11.99 C1:C2	72	0.32
4.	GPP = 14.68 + 6.67 C1:C3	72	0.44
5.	GPP = -16.46 + 13.10 MEAN	77	0.27
6.	GPP = -13.17 + 7.60 MEAN + 13.99 SORT + 0.26 SKEW	77	0.31

benthic primary production, in the range of 60 to 80 mgC m^{-2} hr^{-1} (Figs. 7.21 and 7.22). The highest rate (430 mgC m^{-2} hr^{-1}) was recorded for the low marsh at the intensive study site in Youngs Bay during May 1980, when Enteromorpha was abundant on the sediment surface. This value was atypical of the other observations when microalgae were the only benthic plants. In the intertidal regions, high rates of benthic primary production were found in Youngs Bay in September 1980 (172 mgC m^{-2} hr^{-1}) and October 1980 (156 mgC m^{-2} hr^{-1}), and on a tidal flat in Baker Bay near the town of Ilwaco, Washington, in July 1981 (106 mgC m^{-2} hr^{-1}). The tidal flats in Grays Bay and Cathlamet Bay were less productive than such regions in Baker Bay and Youngs Bay. In Grays Bay and Cathlamet Bay mean rates of gross primary production usually varied between 20 and 40 mgC m^{-2} hr^{-1}, although some of the sandy regions had mean rates less than 20 mgC m^{-2} hr^{-1} (Figs. 7.23 and 7.24). In general, the sandy intertidal areas of the many islands in the study areas exhibited relatively low mean rates of benthic primary production, usually between 10 and 20 mgC m^{-2} hr^{-1}. However, data from the intertidal region on Quinns Island indicated that sandy sites can be productive if sediment disturbance is minimal. In this case, the rate of benthic primary production on the sandy sediments along the upper transect varied from 7 mgC m^{-2} hr^{-1} in June, when freshwater discharge was high, to 109 mgC m^{-2} hr^{-1} in September, when the substrate was relatively undisturbed by water movements.

Comparisons among benthic algal productivities and those of phytoplankton in the Columbia River Estuary study area are difficult because the measurements were, of necessity, made in different ways (Frey et al, 1984; McIntire and Amspoker, 1984). Assuming 1) an annual mean period of 4.2 hrs day^{-1} when light was saturating for benthic algal photosynthesis (see Section 7.1.4), and 2) an annual mean daylight period of 12 hrs day^{-1}, gross benthic algal productivity on an hourly basis at light saturation can be converted roughly to mean gross benthic algal productivity on a daily basis. When this was done using the mean hourly rates for the four regions in Figures 7.21, 7.22, 7.23 and 7.24, mean daily productivities ranged from near zero to about 340 mgC m^{-2} day^{-1}. The areas of highest and lowest daily productivities were also the areas of highest and lowest productivities on an hourly basis. The highest estimate, 340 mgC m^{-2} day^{-1}, was applicable to certain intertidal areas in Baker Bay and Youngs Bay (Figures 7.21 and 7.22). If respiratory losses for benthic algae during the daylight hours averaged 29% of gross productivity (Davis and McIntire, 1983), then the highest net daily benthic primary productivity (340 mgC m^{-2} day^{-1}) would be reduced to about 240 mgC m^{-2} day^{-1}, which was about 60% of the equivalent water-column productilvity for Youngs Bay in July (Figure 7.20). Comparisons in May 1980 were not valid because of the volcanic eruption. In September 1980 the daily phytoplankton productvity in Youngs Bay was comparable only to the areas of lowest mean benthic primary productivity in Youngs Bay.

The estimate of highest mean daily gross benthic algal productivity in Grays Bay and Cathlamet Bay was 170 mgC m^{-2} day^{-1}. Net phytoplankton productivities in July in these two bays were substantially higher (Figures 7.19 and 7.20). In April and September, however, benthic primary productivity was from about 60% to 100% of water column primary productivity, after respiratory losses were subtracted from the daily benthic estimate. Annual primary productivity estimates for the different regions, calculated on a 24-hour basis to remove the effect of different seasonal daylengths, are given in Chapter 8.

Vascular Plants

No direct measurements of short-term emergent plant productvity were made, so the peak biomass data were used to estimate annual above-ground production by the method of Smalley (1958). Above-ground vegetation first appears in the spring of each year, reaches maximum biomass in the summer, then dies back in the late fall (Table 7.5). The Smalley (1958) method does not take into account production lost to grazing by wetland herbivores and lost to the detrital pool through mortality during the peak growing season, and hence the calculation is not the maximum production. However, direct loss to the detrital pool during the growing season was probably minimal in the study area. Loss due to grazing probably was not large on an estuary-wide basis, but might have been significant in localized areas (Macdonald and Winfield 1984).

Estimates of annual above-ground production at each sampling area without considering grazing or mortality losses are given in Table 7.16. Carbon production was assumed to be 40% of production in terms of dry weight (Macdonald and Winfield 1984). The high marsh exhibited higher production rates than the low-marsh in Grays Bay, but there was a tendency toward the opposite in Trestle Bay, due mainly to low-marsh Carex stands. In other regions there was no significant pattern of production by high- or low-marsh location. Outer Youngs Bay was the most productive emergent plant site. Youngs Bay was also the most productive of the benthic microalgal sites (Table 7.13). However, it was one of the least productive of the shallow-water, open-water sites (Figure 7.20).

7.1.6 Process-Generated Outputs

Respiration and excretion of dissolved organic matter are the two metabolic outputs generated by the process of Primary Production (Figure 7.2).

Phytoplankton

Oxidative metabolism, or respiration, by living plants is one mechanism by which biomass is lost from the general pool of photosynthetically produced organic matter in the Columbia River Estuary. Rates of respiration in the estuarine phytoplankton were not measured directly. The carbon-14 technique for measuring phytoplankton productivity presumably measures net, or near net, productivity; thus, respiratory losses during the measurement period are subtracted from photosynthetic accumulation of organic matter by the technique itself. No respiratory corrections were applied to daylight-day estimates of net phytoplankton productivity (Figures 7.19 and 7.20).

Excretion or leakage of dissolved organic matter (DOM) represents

Table 7.16. Net annual primary production of emergent vascular plants in the Columbia River Estuary in 1980, without accounting for the amount consumed by herbivores (see section 7.1.7). L=Low marsh, H=High marsh, M=Middle marsh.

	Net annual primary production	
	g dry wt m^{-2} yr^{-1}	gC m^{-2} yr^{-1}
Baker Bay:		
China Cove _Carex_ (L)	873	349.2
China Cove _Scirpus_ (L)	475	190.0
Ilwaco (L)	850	340.0
Trestle Bay:		
West (L)	861	344.4
West (H)	853	341.2
East _Carex_ (L)	1730	692.0
East (L)	790	316.0
East (M)	1176	470.4
East (H)	803	321.2
Young's Bay:		
Outer (L)	2528	1011.2
Inner (L)	981	392.4
Gray's Bay:		
Outer (L)	641	256.4
Outer (H)	1005	402.0
Inner (L)	545	218.0
Inner (H)	1104	441.6
Cathlamet Bay:		
Army Corps Dock (L)	912	364.8
Lois Island (L)	364	145.6
Russian Island (H)	1094	437.6
Karlson Island (L)	577	230.8
Tronson Island (H)	768	307.2
Fluvial Zone:		
Quinns Island (L)	778	311.2
Puget Island (H)	1502*	600.8*

*=End of season total standing crop

another mechanism, in addition to respiration, by which photosynthetically produced organic matter is lost from living plant cells. Rates of loss of DOM from phytoplankton were not measured in the Columbia River Estuary, however; therefore, no corrections to daily productivity could be made.

Benthic Algae

In benthic communities it is extremely difficult to partition community oxygen uptake into fractions related to respiratory losses from the autotrophs, respiratory losses from heterotrophic macroconsumers and microorganisms, and chemical oxidation of reduced compounds. The physical separation of the autotrophic and heterotrophic constituents of complex, sediment-associated assemblages for respiratory estimates presents a major methodological problem that has not yet been solved by a totally satisfactory approach.

Experimental work with isolated assemblages of epipelic diatoms (Davis and McIntire, 1983) indicated that the mean ratio of net primary productivity to gross primary productivity for liquid suspensions of these organisms was 0.71; thus, respiratory loss during the daylight hours was estimated at 1.00-0.71 = 0.29 or 29% of gross primary productivity. If it is assumed that daylight respiratory rates are the same as night-time rates, the 29% respiratory loss can be applied over a 24 hr period rather than just the daylight period. Gross benthic primary productivity over the daylight period at each of the five intensive sampling sites in the Columbia River Estuary was derived from hourly data in Table 7.13, and reported as GPP (gC m^{-2} day^{-1}) in Table 7.17. The hourly gross primary productivity was then reduced by 29% and multiplied by 24 to yield the 24 hr respiratory rate (AR) of the autotrophs (Table 7.17). Net 24 hr primary production for each of the five intensive sites (NPP) was simply the difference between GPP and AR.

To examine the relationship between autotrophic carbon respiration (AR) and total benthic community carbon metabolism, measurements of community oxygen consumption were taken (McIntire and Amspoker, 1984). Mean hourly rates of oxygen consumption for sediment samples were pooled by month of the year, intensive study site, and tidal level. Assuming a respiratory quotient of unity, these means were then converted to an equivalent carbon loss by multiplying each value by a carbon:oxygen molar ratio of 0.375 (Table 7.18). In general, the pattern of hourly carbon metabolism by the total benthic community at the intensive study sites (Table 7.18) was similar to the pattern observed for hourly gross carbon production (Table 7.13). Multiplication of the mean hourly rates of community metabolism (Table 7.18) by 24 yielded the mean 24 hr rates (OCON) for each intensive study site (Table 7.17). The carbon loss not associated with autotrophs (HR) was the difference between OCON and the estimate of autotrophic respiration (AR). This HR fraction resulted from the respiratory activities of heterotrophic organisms plus any chemical oxidation of reduced compounds. Chemical oxidation of reduced compounds might be indirectly coupled to the metabolic activities of anaerobic microorganisms (Jorgensen, 1977).

The values in Table 7.18 indicated that the sites at Baker Bay,

Table 7.17 Community metabolism at five intensive study sites partitioned by gross primary carbon productivity (GPP), 24 hr carbon respiration by autotrophic organisms (AR), net 24 hr primary carbon production (NPP), carbon equivalents of total benthic community oxygen consumption (OCON), and carbon equivalents of community oxygen uptake not associated with metabolism of autotrophs (HR). The sites are Clatsop Spit (CS), Youngs Bay (YB), Baker Bay (BB), Grays Bay (GB), and Quinns Island (QI). All rates are expressed as gC m^{-2} day^{-1}. Calculations are based on data in Tables 7.13 and 7.18 and on the assumptions given in the text.

Rates	CS	YB	BB	GB	QI
GPP	0.062	1.011	0.510	0.396	0.355
AR	0.036	0.586	0.295	0.230	0.206
NPP	0.026	0.425	0.215	0.166	0.149
OCON	0.163	0.600	0.542	0.403	0.372
HR	0.127	0.014	0.247	0.173	0.166

Table 7.18 Mean rates of carbon respiration (mgC m^{-2} hr^{-1}), sample size, and standard errors of the means for five intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site, and tidal level (transect).

Variable	Sample Size	Mean	Standard Error
Time:			
May	14	24.9	4.8
June	14	19.0	3.9
July	12	21.8	3.5
August	14	21.0	2.5
September	14	22.0	4.5
October	14	15.5	2.5
November	7	18.0	5.3
February	14	9.0	2.5
March	14	18.2	1.8
April	14	14.0	2.0
Site:			
Clatsop Spit	17	6.8	2.0
Youngs Bay	29	25.0	2.7
Baker Bay	29	22.6	2.0
Grays Bay	27	16.8	1.9
Quinns Island	29	15.5	2.1
Tidal Level Transect:			
Marsh (0.9 m above MLLW)	39	23.2	1.9
Upper (0.7m above MLLW)	48	17.6	2.0
Lower (0.3m above MLLW)	44	14.8	1.6

Grays Bay, and Quinns Island might have been close to steady state dynamics, as total consumption (OCON) was only slightly greater than gross primary productivity (GPP). At these sites, values for the ratio GPP/OCON were 0.941, 0.983, and 0.954, respectively, values that were all near unity. Detrital imports could have accounted for the slight heterotrophic tendency. At the Youngs Bay site, GPP/OCON was 1.685, and the system was more autotrophic. These data suggested that benthic plant biomass might have been exported from this site, at least during certain times of the year. In particular, some of the biomass of *Enteromorpha*, which was abundant on the sediment in the low marsh during the spring, was probably transported out of the marsh by water movement. At the Clatsop Spit site, GPP/OCON was 0.383, and the system was more heterotrophic. Detritus was likely imported to the Clatsop Spit site.

Vascular Plants

No process-generated outputs from emergent vascular plants were measured in the current study.

7.1.7 Non-Process Generated Inputs and Outputs

Living plant material is consumed by various grazing organisms, it dies and becomes part of the detritus pool, and in the case of phytoplankton, it is both imported into the estuary and exported from it by river flow and tidal currents (Figure 7.2). Such gains and losses of biomass are not generated by the process of Primary Production.

Phytoplankton

Consumption of Phytoplankton

Consumption of living phytoplankton by grazing organisms is difficult to evaluate when consumers are feeding on complex mixtures of living and non-living particles in the water column. The approach taken in the Columbia River Estuary involved using carbon-14 to label viable cells and then measuring 1) the uptake of the radiocarbon into the zooplankton grazing on the labelled cells, and 2) the disappearance of labelled cells from the cell concentration being grazed. From these data, zooplankton filtration rates were computed, in units of volume (ml) of water filtered per animal per hour. Multiplication of hourly rates by 24 yielded estimates of daily rates, assuming the animals filtered water continuously every 24-hour period. This assumption likely was not valid, so the daily filtration rates were probably overestimated to some unknown degree.

Mean daily filtration rates for the three most abundant taxa in the estuary for June and July 1981 are given in Table 7.19. A reasonable estimate of the mean filtration rate for the composite microcrustacean community over the whole estuary was 1.2 ml animal^{-1} day^{-1}. Because *Bosmina longirostris* was considered a minor fraction of the yearly zooplankton community composition, its filtration rate was not considered in the mean. The filtration rates in Table 7.19 were similar to other values reported in the literature for zooplankton species found in the Columbia River Estuary (Richman, 1958; Nauwerck, 1959, 1963;

Marshall and Orr, 1962; McQueen, 1970; Haney, 1973; Taguchi and Fukuchi, 1975).

Daily filtration rates multiplied by the concentrations of phytoplankton carbon and grazing zooplankton in the water will yield daily rates of removal of phytoplankton carbon by grazers. Concentrations of grazing zooplankton were not measured for each estuarine region (Jones and Bottom, 1984), but reasonable estimates for the total estuary for different months were assembled by Frey et al. (1984). Using these estimates, coupled with daily filtration rates and mean phytoplankton carbon estimates for the whole estuary by sampling month (derived from Figures 7.9 and 7.10), mean daily loss of phytoplankton carbon due to grazing was calculated (Table 7.20). Grazing loss was an order of magnitude greater in spring and summer than in fall and winter, due principally to the greatly reduced numbers of zooplankton in the colder months. Grazing loss was a smaller fraction of phytoplankton productivity during fall and winter than during spring and summer, even though rates of primary production in fall and winter were themselves very small (Figures 7.19 and 7.20). Grazing loss did not represent a large removal of phytoplankton biomass at any time of year. Even though all potential grazers were not evaluated (certain larval fish, for example), the percentages of primary productivity represented by grazing loss were not expected to differ much from those listed in Table 7.20 because microcrustacean zooplankters were the dominant suspension feeders in the Columbia River Estuary.

Natural Mortality of Phytoplankton

Natural mortality of primary producers is defined as all losses of plant biomass not grazed away or exported out of the estuary as living, photosynthesizing tissue. Plant material that dies enters the detrital pool, and is considered lost from the Primary Production subsystem.

The great decline in chlorophyll a concentration, particularly in late spring and summer, that occurred between the Cathlamet Bay region (region 7) and the mixing zone (regions 3 + 5), and to a lesser extent between regions 8 and 7 and between 3 + 5 and 1 was largely attributed to death of freshwater phytoplankton cells as they encountered brackish water (Figure 7.9). The decline clearly was too large to be accounted for by grazing loss and/or differential import of chlorophyll a from tributaries. Although Deep River had high concentrations of chlorophyll a in September 1980 (Figure 7.10), its volume of flow into Grays Bay was insignificant, and concentrations in Grays Bay were about the same as those in the middle estuary regions. Net natural mortality of phytoplankton in the Columbia River Estuary thus was considered as the total loss of chlorophyll, minus any measured chlorophyll losses due to grazing and export out of the mixing zone. The natural mortality loss enters the detritus pool.

Chlorophyll a concentrations in regions 8, 7, 3 + 5 and 1 for all sampling months in 1980 were converted to phytoplankton carbon concentrations (PPOC) by employing the carbon:chlorophyll a ratio of 40 (Table 7.21). In addition, the ratios of PPOC to total particulate organic carbon in the water column (TPOC) were calculated. TPOC was

Table 7.19. Mean filtration rates for the three most abundant taxa in the estuary, ± one standard error. n = six animals per station.

Group	Station		$(\text{ml animal}^{-1}\text{day}^{-1})$ June	July
Copepods (mixed)	501		1.03 ± 0.25	1.62 ± 0.25
Copepods (mixed)	451		1.00 ± 0.13	0.93 ± 0.40
Copepods (mixed)	201		1.10 ± 0.24	1.53 ± 0.31
		Mean	1.04 ± 0.20	1.36 ± 0.32
Bosmina longirostris	501		0.61 ± 0.24	
Bosmina longirostris	451		0.32 ± 0.03	
Bosmina longirostris	201		0.55 ± 0.19	
		Mean	0.49 ± 0.15	
Daphnia spp.	451			1.26 ± 0.32
Daphnia spp.	201			1.19 ± 0.22
		Mean		1.22 ± 0.27

Table 7.20. Mean daily loss of phytoplankton carbon from the Columbia River Estuary as a result of grazing, for each month of sampling except May 1980 (the effects of the volcanic eruption invalidated the estimates for May 1980).

Month	Grazing Loss	
	MgC m^{-2} day^{-1}	% of Primary Productivity
February	0.32	0.6
April	10.54	6.3
May	-----	---
July	17.56	2.2
September	0.73	0.3
November	0.45	0.7

measured at many stations during all cruises by combusting particles filtered from known volumes of estuary water in an elemental analyzer. The PPOC values were then used to compute carbon transports (imports and exports) between regions 8, 7, 3 + 5, and 1 (see Import and Export of Phytoplankton, this Section). Natural mortalities (M) for each region between Regions 8 and 1 were then calculated for each sampling month as

$$M_r = (P_r + I_r) - (G_r + E_r)$$

where P_r is mean phytoplankton carbon productivity in region r, I_r is mean phytoplankton carbon import into region r, G_r is mean grazing removal of phytoplankton in region r, and E_r is mean phytoplankton carbon export from region r. Summation of the regional mortalities yielded an estimate of total phytoplankton mortality from region 8 to region 1. Appropriate volume conversions allowed expression of total natural mortality as mgC m^{-2} day^{-1} (Table 7.21).

Natural mortality was large, and increased from lowest rates in late winter (February) to highest rates in midsummer (July). The identical trend was observed for the much smaller grazing mortality (Table 7.20). Neither the maximum grazing mortality nor the maximum natural mortality coincided in time with the maximum phytoplankton carbon concentration in the water, however. Maximum PPOC occurred in May, 1980 in all regions, as a result of phytoplankton import created by the Mount St. Helens eruption (Table 7.21). Maximum PPOC in May coincided with one of the lowest PPOC:TPOC ratios in regions 7 and 8, however, indicating a large detrital component of the enormous TPOC concentration following the volcanic blast. A higher PPOC:TPOC ratio would normally have been expected in May in regions 7 and 8, perhaps intermediate to the April and July ratios (Table 7.21).

Natural mortality calculated as above implied net loss from the water column. However, loss of chlorophyll a might not have represented disappearance of particulate carbon. Fluorometric or spectrophotometric methods for detecting chlorophyll a would have shown a decline in particulate chlorophyll a concentration as cells lysed on encountering saline waters, but phytoplankton-derived carbon might not have shown a concomitant decline. Thus, as the living phytoplankton died and became detrital particles, total particulate carbon concentration in the water column might not have changed, even though the chlorophyll a concentration, and hence living phytoplankton biomass, decreased.

Import and Export of Phytoplankton

Import and export of living primary producers are non-process-generated inputs and outputs, respectively. These terms mainly involve the phytoplankton, the only living, free-floating plant material in the Columbia River Estuary. Mixing of living benthic algal cells into the water column did occur in the study area, particularly over mudflats during tidal inundation, but the functional attributes of these cells were evaluated with the phytoplankton during measurements of primary production. Similarly, true phytoplanktonic cells undoubtedly settled onto substrates and continued to metabolize, and in quantitative measurements such cells were considered benthic microalgae. Non-living

Table 7.21. Concentrations of living phytoplankton carbon (PPOC), and PPOC as a fraction of total particulate organic carbon (TPOC) in regions 8, 7, 3+5, and 1 of the Columbia River Estuary. Daily natural mortality between regions 8 and 1 was also estimated for each sampling month.

	PPOC (mgC m^{-3})				PPOC:TPOC				Natural Mortality
Month	Region 8	Region 7	Region 3+5	Region 1	Region 8	Region 7	Region 3+5	Region 1	(mgCm^{-2} day^{-1})
Feb	220	189	130	57	0.27	0.23	0.16	0.07	134.4
Apr	284	254	205	164	0.31	0.28	0.23	0.18	262.5
May	652	612	440	333	0.12	0.11	0.08	0.06	504.2
July	488	456	210	212	0.42	0.40	0.18	0.18	1124.9
Sept	328	247	140	55	0.23	0.18	0.10	0.04	274.9
Nov	216	166	95	75	0.14	0.11	0.06	0.05	173.4

cells, plants, or plant fragments, regardless of origin, were part of the detritus pool, and their imports and exports are considered in Section 7.2.

Transport of phytoplankton biomass from upriver to the sea can be estimated by calculating chlorophyll transports through region 8 and then, in sequence, through regions 7 and 3 + 5. Transport through region 1 to the ocean could not be estimated because of the lack of chlorophyll data in the adjacent ocean. A two-parameter model based on salt transport, which assumed complete vertical mixing along the length of the river-estuary continuum, was used to evaluate horizontal exchange between each adjacent region (Officer, 1980; Jay, personal communication). The parameters required to estimate the exchange rates are shown in Figure 7.25. The governing equations for estimating the exchange rates between regions 8 and 7 (E_{87}), 7 and 3 + 5 ($E_{7(3+5)}$), and 3 + 5 and 1 ($E_{(3+5)1}$) are:

$$Q_0S_8 = E_{87}\ (S_7 - S_8),\ \text{or}\ E_{87} = Q_0S_8/(S_7 - S_8)$$

$$Q_0S_7 = E_{7(3+5)}(S_{(3+5)} - S_7),\ \text{or}\ E_{7(3+5)} = Q_0S_7/(S_{(3+5)} - S_7)$$

$$Q_0S_{(3+5)} = E_{(3+5)1}\ (S_1 - S_{(3+5)}),\ \text{or}\ E_{(3+5)1} = Q_0S_{(3+5)}/(S_1 - S_{(3+5)}),$$

where Q_0 is river flow ($m^3\ sec^{-1}$), S is salinity ($^o/oo$), and E is the exchange between regions ($m^3\ sec^{-1}$). The subscripted numbers refer to the specific regions. Evaluations of all parameters are given in Table 7.22 for high-flow sampling months (April and May), low-flow months (July and September), and winter months (November and February). Best estimates of river flows and salinities were made from data in Chapters 2 and 3.

Because salinity was zero in the freshwater regions, exchange between regions 8 and 7 and between regions 7 and 3 + 5 was zero. Transport thus was governed solely by riverflow (Q_0) and chlorophyll concentration (C). For example, import of phytoplankton chlorophyll into region 7 from region 8 was:

$$T_{87} = Q_0C_8,$$

where T is chlorophyll transport (mg sec^{-1}) and C_8 is chlorophyll concentration (mg m^{-3}) in Region 8. Chlorophyll transport into the Entrance Region (region 1) was calculated from:

$$T_{(3+5)1} = Q_0C_{(3+5)} + E_{(3+5)1}\ (C_{(3+5)} - C_1).$$

Mean chlorophyll a concentrations by region are shown in Figure 7.9 for the months of the year in which samples were taken. Conversion of

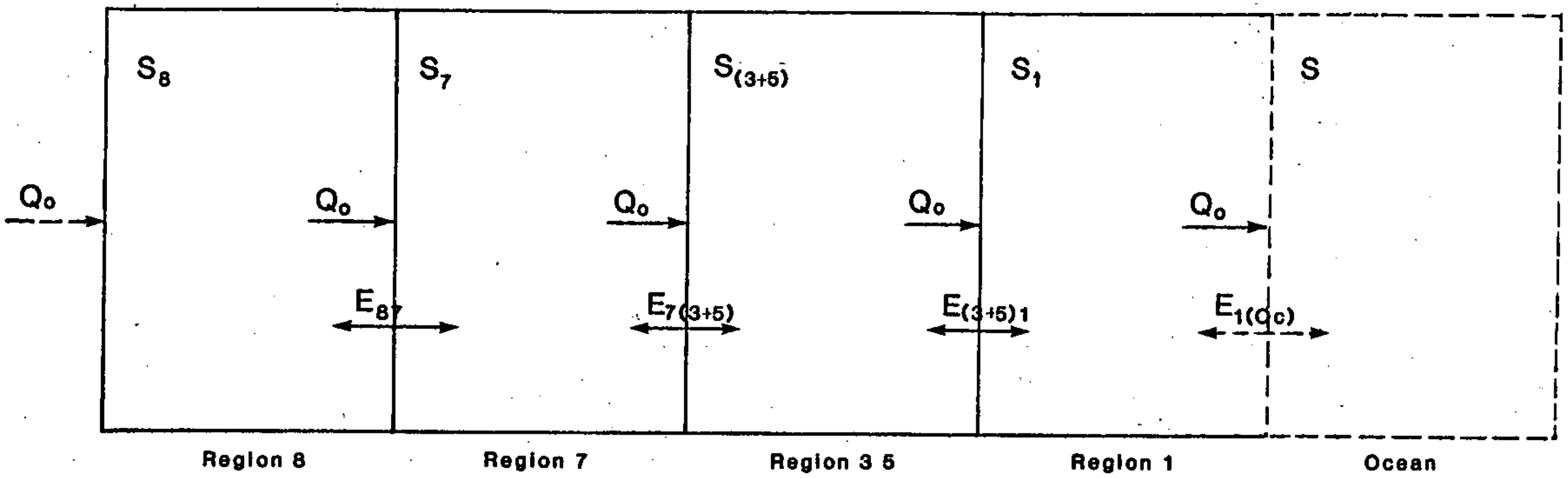


Figure 7.25. Two-parameter model of the Columbia River estuarine continuum, used to evaluate horizontal exchanges between adjacent regions (based on salt transport). S = salinity ($^o/oo$), Qo = river flow (m^3 sec^{-1}). The E terms are used to calculate transport of phytoplanktonic chlorophyll a through the estuary. Exchange between Region 1 and the adjacent ocean can be calculated roughly from existing data, but chlorophyll transports cannot be calculated because no chlorophyll a concentration data are available in the adjacent ocean for the appropriate months and years (hence dashed lines outline the Ocean region).

Table 7.22. Values for parameters used to estimate exchange rates (E) between regions, and computed values of E (m^3 sec^{-1}) between upriver, Regions 8, 7, 3+5 and 1, and the ocean. Salinities are averages of high-flow, low-flow, and winter periods. See text for further data.

Parameter	(Units)	Apr.80	May 80	July 80	Sept.80	Nov.80	Feb.81	Apr.80
Q_o	(m^3 sec^{-1}x10^3)	9.2	10.7	6.0	2.7	4.0	7.4	7.2
S_8	(°/₀₀)	0	0	0	0	0	0	0
S_7	(°/₀₀)	0	0	0	0	0	0	0
$S_{(3+5)}$	(°/₀₀)	5.67	5.67	9.66	9.66	6.50	6.50	5.67
S_1	(°/₀₀)	15.24	15.24	23.80	23.80	16.50	16.50	15.24
E_{08}	(m^3 sec^{-1}x10^3)	0	0	0	0	0	0	0
E_{87}	(m^3 sec^{-1}x10^3)	0	0	0	0	0	0	0
$E_{7(3+5)}$	(m^3 sec^{-1}x10^3)	0	0	0	0	0	0	0
$E_{(3+5)1}$	(m^3 sec^{-1}x10^3)	5.45	6.34	4.10	1.84	2.60	4.81	4.27

these values to carbon concentrations and use of the parameters in Table 7.22 allowed calculation of phytoplankton carbon transports (Table 7.23). Transport rates decreased from region 8 through regions 3 + 5 on all sampling dates. In some months the exchange term in the transport equation minimized the effect of a sharp decline in phytoplankton concentration; for example, in May 1980, chlorophyll *a* concentrations exhibited a sharp decline between region 7 and regions 3 + 5 (Figure 7.9), but the decline in transport between the two regions was not so precipitous (Table 7.23). In July 1980, however, the decline in chlorophyll *a* concentration between regions 7 and 3 + 5 (Figure 7.9) was a manifestation of the decline in transport between the two regions (Table 7.23).

Benthic Algae

No data on consumption of benthic algae by consumers were available for the Columbia River Estuary, and no data on algal death and subsequent transfer to the detritus pool were available. No import or export terms for live benthic microalgae have been considered.

Vascular Plants

Consumption of Vascular Plants

The only non-process-generated biomass losses were those due to grazing and natural mortality. Muskrat, nutria and beaver were the primary herbivores consuming marsh plant biomass in the Columbia River Estuary. The best range of estimates of above-ground plant consumption in the estuary by muskrats was 506 to 4,455 MT yr^{-1}, on a fresh weight basis (Merker and Fenton 1984). This was equivalent to a range of 40 to 356 MT C yr^{-1}. Above-ground plant consumption by nutria ranged between 3,973 and 33,062 MT yr^{-1}, on a fresh weight basis (Merker and Fenton 1984), or about 318 to 2,645 MT C yr^{-1}. Consumption by beaver ranged between 176 and 200 MT fresh plant weight yr^{-1}, or 14 to 16 MT C yr^{-1}. Most food consumption by beaver took place in the high marsh and swamp areas, while muskrat and nutria ate primarily in low marsh regions and sometimes in the high marsh. Columbian white-tailed and black-tailed deer consumed an estimated 8 to 11 MT C yr^{-1}, but not all was removed from high and low marsh regions of the estuary. In addition, dabbling ducks (particularly mallards) and herbivorous insects must have consumed a measurable portion of marsh plant biomass, but estimates were not available.

Muskrat, nutria and beaver together consumed approximately 372 to 3,017 MT of plant carbon annually. This was net production that had been removed but not measured by the Smalley (1958) method. Therefore, on average, total annual estuarine marsh plant production, obtained by expanding per-square-meter carbon estimates derived from Table 7.16, should have been increased by the annual amount consumed. Consumption represented about 3 to 21% of emergent plant carbon production after measured production was increased by the amount consumed. A reasonable estimate of mean annual consumption would be 10% of annual primary carbon production, or possibly 15% if consumption by deer, dabbling ducks, insects and any other herbivore is considered. This estimate

Table 7.23. Daily transport of phytoplankton carbon through regions of the Columbia River Estuary, for each sampling month.

Month	Transport Rates (Mt C day^{-1},		
	Region 8	Region 7	Regions 3 + 5
February	140.7	120.8	113.5
April	225.8	201.9	182.3
May	602.8	565.8	465.4
July	253.0	236.4	91.2
Sept	76.5	57.6	46.2
Nov	74.7	57.4	37.3

represented a greater fractional removal than the fraction established for small grazers in the water column (Table 7.20). Certain marsh regions of the estuary might have been grazed much more heavily than the mean percentage, of course, even to the point of complete decimation of above-ground vegetation, while other areas might not have been touched. Certain plant species in the marshes were known to be preferred foods (Dunn et al. 1984), while other species were seldom eaten.

Below-ground plant material was consumed during winter by furbearers, but no estimate of this consumption was made here because it did not directly affect annual above-ground production in the marshes.

Natural Mortality of Vascular Plants

Much of the above-ground vascular vegetation died back and entered the detrital pool in winter, so that natural mortality probably approximated total peak biomass in summer (Macdonald and Winfield, 1984). However, biomass removed by herbivores, and organic material translocated in the fall from above-ground vegetation to roots, was not natural mortality, and must be accounted for if significant. No direct measurements of translocation to roots were made for emergent plants of the Columbia River marshes; however, Kistritz *et al.* (1983) estimated that 38% of the peak emergent plant biomass in a *Carex*-dominated tidal marsh of the Fraser River Estuary, British Columbia, was translocated to roots in autumn. If herbivore grazing removed an average of 15% of annual production and translocation removed 38% of peak biomass in the Columbia River Estuary, then annual biomass removal to the detrital pool via natural mortality was 47% of annual production.

7.1.8 Annual Production Dynamics

Annual primary production of phytoplankton, benthic algae and vascular plants can be compared when all production estimates are put into comparable units. Because vascular plant production was resolved on an annual basis, the phytoplankton and benthic algal productivity estimates had to be scaled up to annual estimates. Net production in terms of gC m^{-2} yr^{-1} for phytoplankton, benthic algae and vascular plants was used to compute estimates of primary production for the entire Columbia River Estuary and for each region within the study area (see Chapter 8).

Phytoplankton

Annual estimates of net primary production in the water column (gC m^{-2} yr^{-1}) were made for the regions in Figure 7.1. Mean daily productivities for each region and each sampling month, available as both measured and predicted values (Figures 7.19 and 7.20), were expanded to monthly productivities by simply multiplying by the number of days in each month. For months in which no samples were taken, extrapolations were made using solar radiation data. For example, the mean of July and September productivities divided by the mean monthly light inputs yielded a value of productivity per unit of light. When this value was multiplied by the mean solar radiation input for August 1980, a monthly productivity for August was generated. Estimates done in this manner, while not precise, nevertheless were considered satisfactory because light was the major limiting factor to water-column primary productivity (Tables 7.11 and 7.12). Once monthly production values were calculated for each region, they were added to give annual per-square-meter production for each region (Table 7.24). Nighttime respiration estimates were made and subtracted from daytime rates to yield 24-hr based estimates of net production (Table 7.24). Total annual production for each region, obtained by multiplying by the area (m^2) of water surface in each region, is reported in Chapter 8.

A steady decrease in annual areal production from the Fluvial Region to the Entrance Region was evident in the main body of the Columbia River Estuary; that is, production decreased from region 8 to 7 to 3 to 1 (Table 7.24). The two bays (Youngs and Grays) had the smallest areal production. Although not listed in Table 7.24 because of their small areas, the tributary rivers had high areal productivities. As indicated earlier, these productive tributaries flowed into the relatively unproductive Youngs Bay and Grays Bay (Table 7.24), supporting the idea that primary production was measurably affected as freshwater phytoplankton assemblages in the tributaries met the brackish waters of the bays.

Benthic Algae

Extrapolating benthic algal hourly productivity data (Table 7.13 and Figures 7.21, 7.22, 7.23 and 7.24) to estimates of annual rates was a difficult problem that required explicit assumptions relating to light intensity at the water surface, light attenuation in the water column, and tidal inundation time. The approach taken here applied to the intertidal region from MLLW to the edge of the low marsh. The assumptions were: 1) the annual mean value for the light attenuation coefficient $\underline{k}$ in the water over the tidal flats was 2.75; 2) maximum photosynthesis was attained at a light intensity of 400 uE m^{-2} sec^{-1}; and 3) the mean light intensity at the water surface during daylight hours was 1,428 uE m^{-2} sec^{-1}.

From the assumptions above, the maximum water depth (Zmax) at which photosynthesis could have occurred at its light-saturated rate was

$$\text{Zmax} = \frac{\ln\ (400/1428)}{-2.75} = 0.46\ \text{m.}$$

The sampling transects at the intensive study sites in the intertidal region were at 0.3 m (lower), 0.5 m (mid), and 0.7 m (upper) above MLLW. Therefore, maximum photosynthetic rates by benthic algae still could have occurred along these transects when water levels were approximately 0.5 m higher than the transect levels, or less (i.e., when water levels reached 0.8 m, 1.0 m, and 1.2 m above MLLW at the lower, mid, and upper transect levels, respectively). From tidal inundation data for seven locations in the estuary, the benthic algal communities at the lower, mid, and upper transect levels were exposed to saturating light for mean periods of 6.45, 8.43, and 10.43 hr day^{-1}. Assuming that a mean value for the three transects was a reasonable estimate for the entire tidal flat, the mean number of hours per day at which the water level was less

Table 7.24 Annual rates of net phytoplankton production (gC m^{-2} yr^{-1}) by region, for the daylight period only and for the full 24- hour period with nighttime respiration subtracted. The estimate for region 2 was taken as a mean of daylight productivities in regions 1 and 4.

Region	gC m^{-2} yr^{-1} (daylight rates only)	gC m^{-2} yr^{-1} (with nighttime respiration subtracted)
(1) Entrance Region	69.3	41.0
(2) Baker Bay and Trestle Bay	61.5	41.5
(3) Estuarine Channels	84.9	50.2
(4) Youngs Bay	53.7	31.8
(5) Mid-Estuary Shoals	84.9	50.8
(6) Grays Bay	66.3	39.2
(7) Cathlamet Bay	104.7	61.9
(8) Fluvial Region	121.0	71.6

than or equal to a height that could allow maximum photosynthesis was 8.44 hr day^{-1}. With a mean daylength for the entire year of approximately 12 hours, or one-half of the 24-hr day, an estimate of the mean number of hours per day during the year that benthic plants were exposed to enough light to support the light-saturated rate of photosynthesis was only 0.5 x 8.44 = 4.22 hr. Because benthic microalgal assemblages reach the light-saturated photosynthetic rate very rapidly with increasing light intensity, and all mean hourly rates measured for the study sites were light-saturated rates, a rough estimate of the mean annual light-saturated rate for a particular tidal flat could be obtained by multiplying the mean hourly rate by 4.22 hr day^{-1} and 365 days yr^{-1}.

Estimates of annual rates of gross benthic primary production are given in Table 7.25. Mean rates for the survey sites ranged from about 23 to 97 gC m^{-2} yr^{-1}, and for the intensive study sites the range was about 8 to 121 gC m^{-2} yr^{-1}. The gross production values were very similar to values reported by other investigators for various geographical locations (Table 7.26).

To estimate annual rates of net benthic primary production from direct measurements of gross primary production, it was assumed that the respiratory losses by autotrophic organisms were 29% of gross primary production during the daylight hours. Also, it was assumed that respiratory losses during the dark hours of the day were equal to such losses during the daylight hours. The estimates of net benthic 24-hr-based production (Table 7.25) were similar to those for 24-hr water column production (Table 7.24) in the Youngs Bay and Baker Bay Regions, but were much less than the water-column production estimates in the Grays Bay, Cathlamet Bay and Fluvial Regions.

Vascular Plants

Estimates of above-ground vascular plant production, in terms of gC m^{-2} yr^{-1}, are given in Table 7.16. It is obvious that annual vascular plant production on a per-square-meter basis in most marsh regions was much higher than either water-column (Table 7.24) or benthic (Table 7.25) algal production.

Estimates for the Entire Estuary

The total estuarine study area under investigation was 41,182 hectares. The total estimated net primary production for the region was approximately 30,000 metric tons of carbon per year. This total was determined by summing the estimated contributions from the benthos, marshlands, and water column for the eight major regions in the study area (the tributary rivers were excluded). Of the 30,000 MT C yr^{-1}, the contributions from benthic plants, emergent vascular plants, and phytoplankton were 1,545 MT (5%), 11,324 MT (38%), and 17,115 MT (57%), respectively. These production data are partitioned by region and habitat type in Chapter 8.

Table 7.25. Annual rates of gross and estimated benthic net primary production (with nighttime respiration subtracted) expressed as gC m^{-2} yr^{-1} for the intensive study sites and the survey sites grouped by region. Gross production values are based on direct measurements of hourly rates (intensive study sites) and hourly rates predicted from the concentration of chlorophyll *a* in the top cm of sediment (survey sites). Gross production was converted to net production and hourly rates were converted to annual rates by the procedures described in the text.

Location	Gross Primary Production		Net Primary Production	
	Mean	Range	Mean	Range
Intensive Study Sites:				
Clatsop Spit	8.0	0.0-36.5	3.4	0-15.3
Youngs Bay	120.9	0.0-264.3	50.8	0-111.0
Baker Bay	69.3	0.0-152.7	29.1	0-64.1
Grays Bay	44.6	0.0-120.0	18.1	0-50.4
Quinns Island	33.5	0.0-167.2	14.1	0-70.2
Survey Sites:				
Baker Bay Region	97.2	8.6-156.3	40.8	3.6-65.6
Youngs Bay Region	71.2	30.3-101.6	29.9	12.7-42.7
Grays Bay Region	25.9	16.5-37.2	10.9	6.9-15.6
Cathlamet Bay Region	22.6	15.6-33.6	9.5	6.6-14.1
Fluvial Region	38.3	15.7-63.9	16.1	6.6-26.8

Table 7.26. Some annual rates of gross (G) and net (N) benthic primary production determined by different investigators for various geographical locations.

Study	Location	Rate	
1. Steele & Baird (1968)	Scotland, exposed beach	4 - 9	(N)
2. Pomeroy (1959)	Georgia salt marsh	200	(G)
3. Grontved (1960)	Danish fjords	116	(N)
4. Cadee & Hegeman (1977)	Western Wadden Sea	29-188	(N)
5. Pamatmat (1968)	Falsee Bay, San Juan Island	143-226	(G)
6. Gallagher & Daiber (1974)	Delaware salt marsh	38-99	(G)
7. Marshall et al. (1971)	Southern New England estuarine shoals	100	(G)
8. Leach (1970)	Northern Scotland mudflat	31	(N)
9. Riznyk & Phinney (1972)	Yaquina Estuary, Oregon:		
	sandy silt	275-325	(G)
	fine silt	0-125	(G)
10. Davis & McIntire (1983)	Netarts Bay, Oregon:		
	sand	129	(G)
	sandy silt	153	(G)
	silt	72	(G)

7.2 PRIMARY FOOD PROCESSES: DETRITAL DECOMPOSITION

7.2.1 Introduction

Model and Couplings

Detritus accumulates in the Columbia River Estuary directly as a result of the death of autotrophic and consumer organisms, and indirectly as a result of import of detritus and production of fecal matter (Figure 7.26). Because detritus is considered for analytical purposes as all dead particulate organic matter plus its associated heterotrophic microflora and microfauna, nutrients can stimulate detrital decomposition by stimulating microfloral and microfaunal growth.

Detritus can accumulate in the estuary, can be eaten, or can enter or leave the estuary through import or export. Consumer processes can also mechanically break particles, thereby accelerating decomposition. Other losses occur through microfloral and microfaunal consumption and the concurrent respiration and excretion of dissolved organic compounds.

Data Base

Particulate detritus suspended in the water column, from whatever source, was not measured directly, but was computed as the difference between total particulate organic carbon (TPOC) and phytoplanktonic carbon (PPOC), and from particulate-carbon:nitrogen (TPOC:TPON) ratios. A detrital component from benthic microalgae was computed as the difference between total ash-free dry weight and estimates of algal ash-free dry weight. Litter bag studies of emergent vascular plant material yielded information on decomposition rates for large plant remains which would ultimately add to the detrital suspensoids in the water.

Some mortality rates of a few macroconsumer organisms were estimated, and these data related to the rate at which animal biomasses entered the detrital pool in the Columbia River Estuary. Carcasses of zooplankton and small benthic fauna likely contributed significantly to the detrital pool, but unfortunately no mortality estimates were available. Also, significant detrital inputs such as fecal matter from the smallest to the largest animal species, and molts from certain zooplanktonic and benthic animals, were not measured in a quantitative way. However, a few estimates were attempted for selected macroconsumers.

No data were available on the separation of detritus from the decomposer organisms associated with it; therefore, there were no data on excretion of dissolved organic matter by the micro-organisms, and no data on nutrient uptake by these detrital-associated microbes. Some indirect estimates of heterotrophic respiration in sediments were available, and such respiration probably was derived from detritus-associated heterotrophs.

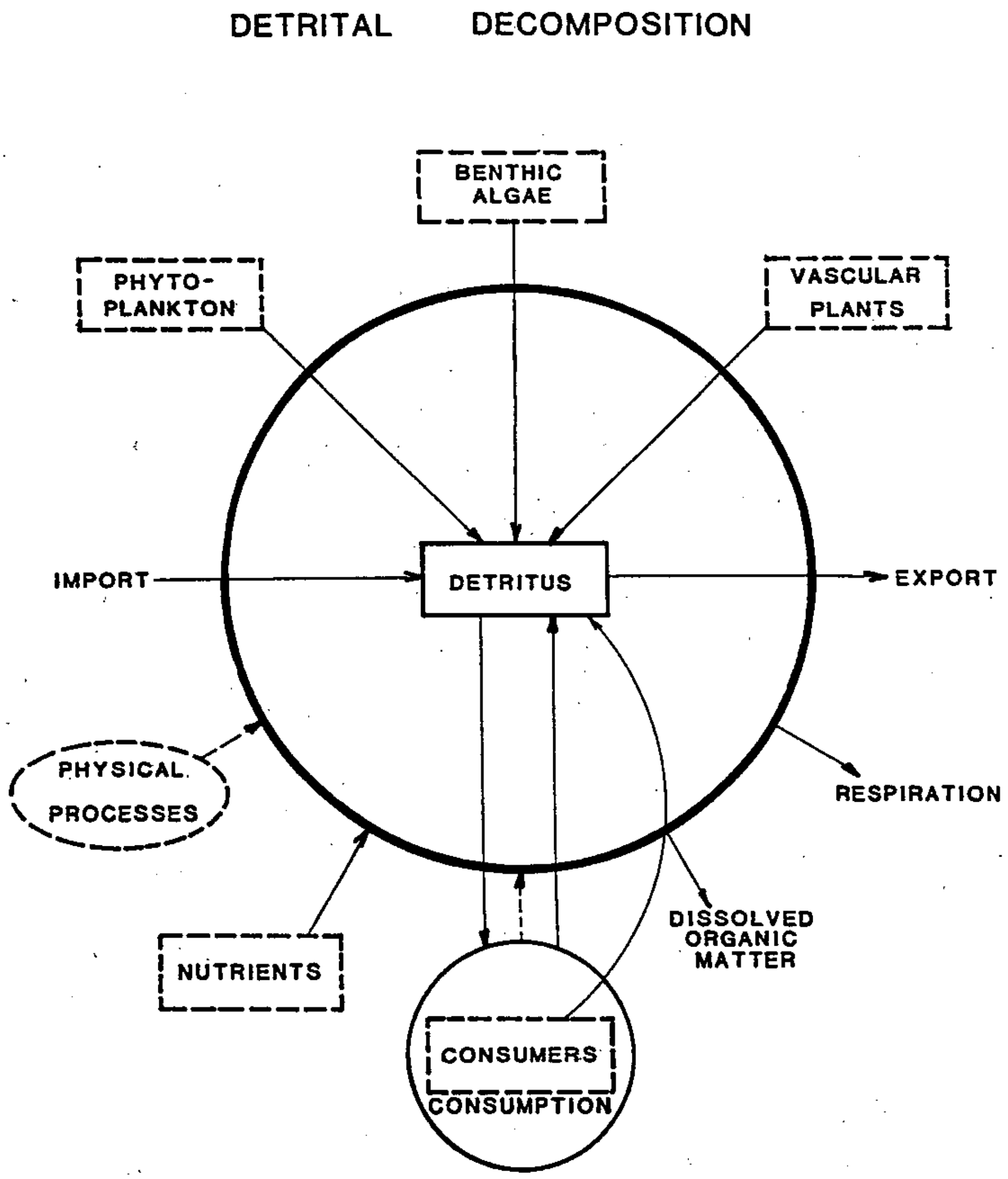


Figure 7.26. Detrital Decomposition, a subsystem of Primary Food Processes.

7.2.2 Detrital Biomass

Water Column

Subtraction of phytoplankton-associated carbon (PPOC) from total particulate organic carbon (TPOC) yielded an estimate of detrital particulate organic carbon (DPOC). Mean concentrations of DPOC for regions 8, 7, 3 + 5, and 1 for each month of sampling were computed (Table 7.27). In addition, the ratios DPOC:TPOC were listed for each month. DPOC represented from 58 to 88% of TPOC in region 8; however, DPOC in region 1 was 82 to 96% of TPOC. Living phytoplankton apparently was being converted to detrital carbon, and/or more detrital carbon was being mixed into the TPOC pool, as the TPOC was being transported downstream. Although the concentrations of DPOC in May 1980 were very high as a result of the volcanic eruption, the DPOC:TPOC ratios were not unusual in comparison with other ratios throughout the year. The May 1980 ratios in all four regions were higher than the April and July ratios, however. In other estuarine systems DPOC has also been reported to be the dominant suspended fraction (Parsons and Takahashi, 1973; Poulet, 1976; Chervin, 1978; Raymont, 1980).

As Redfield et al. (1963) have noted, the TPOC:TPON ratio in live phytoplankton, by atoms, is approximately 6.6. By weight the ratio is 5.7. In the data for the Columbia River Estuary (Figure 7.27) there were no ratios as low as 5.7, but freshwater values at all times of year (except May 1980), and most values in winter and early spring throughout the estuary, were below 10. Ratios below 10 suggested a significant contribution by live cells. The mixing zone (generally regions 3+5) in summer, however, had high TPOC:TPON ratios (up to 25), indicating that detrital carbon was being concentrated in this zone. Concentration of detrital particles in the mixing zone, concomitant with a loss of chlorophyll *a* in the mixing zone in summer (Figures 7.9), again suggested that live freshwater phytoplankton died (or at least lost their chlorophyll) in this region of the estuary, and were replaced or augmented by non-living carbonaceous detrital particles mixed into the water column from the estuary near-bottom waters.

Tidal Flats

The living algal biomass in the top centimeter of sediment at the intensive study sites was estimated by multiplying chlorophyll *a* concentration by the AFDW:Chlorophyll *a* ratio of 167 (Davis and McIntire, 1983). Subtraction of the living biomass from total AFDW provided an estimate of detrital biomass expressed as AFDW m^{-2} in the top centimeter of sediment. Then, assuming detrital carbon was 50% of detrital AFDW (McIntire and Amspoker, 1984), the mean annual detrital carbon (DPOC) and the corresponding DPOC:TPOC ratios were computed for the top centimeter of sediment in the marsh, upper and lower transects of each intensive study site (Table 7.27).

The range of DPOC:TPOC in the water column was 0.58 to 0.96 over the year, depending on season and location in the study area (Table 7.27), while the range in the sediment was 0.74 to 0.97, depending on location in the estuary (Table 7.28). This similarity occurred even

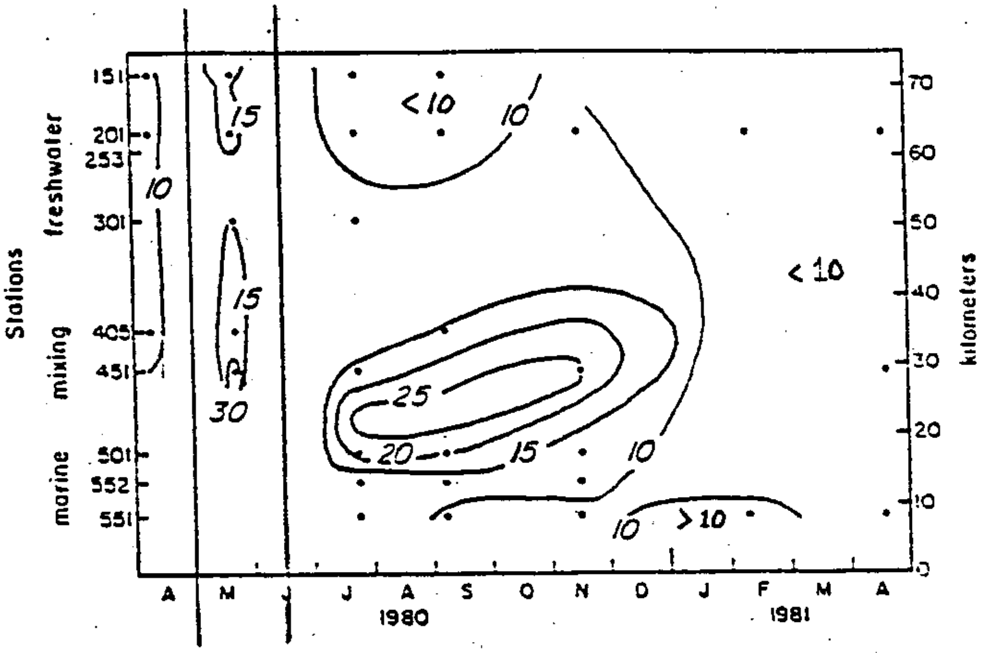


Figure 7.27. Spatial-temporal distribution of particulate organic carbon: particulate organic nitrogen ratio. The two vertical lines separating May and one half of June 1980 from other months isolate the time period over which Mt. St. Helens volcanic debris was evident in the water column.

though the absolute concentrations of DPOC and TPOC in the two environments usually differed markedly. The mean annual DPOC concentration in the water column in region 8, excluding the May 1980 data (Table 7.27), was 888 mgC m^{-3}. Region 8 had the highest fraction of DPOC. If the depth over which this average concentration applied was 10 m (a reasonable water depth for the navigation channel), then DPOC concentration through the water column averaged 8,880 mgC m^{-2}, or approximately 8.9 gC m^{-2}. The lowest DPOC concentration in the tidal flat transects was 27.4 gC m^{-2} along the upper transect at Clatsop Spit (Table 7.28), and this concentration was only for the top centimeter of sediment. Even if sediments below the top cm contained less detrital organic carbon than 27.4 gC m^{-2}, the concentrations still likely would have been much higher than any water column concentration.

The similar DPOC:TPOC ratios in the water column and the sediments strongly suggested that the dilute detrital suspensions in the water column had origins similar to the denser detrital concentrations in tidal flat sediments. This was not unexpected. Strong support for a common allochthonous detrital origin came from the May 1980 water-column data. After the Mount St. Helens eruption, the measured DPOC concentrations ranged from 4,781 to 5,214 mgC m^{-3} (Table 7.27). Multiplying these concentrations by a 10 m average water-column depth yielded 47,810 to 52,140 mgC m^{-2}, or approximately 47.8 to 52.1 gC m^{-2}, most of which was delivered from tributary rivers into the main body of the Columbia River Estuary as a direct result of watershed scouring by the volcanic debris. This May 1980 DPOC concentration was higher than the Clatsop Spit sediment concentrations, and as high or higher than two of the Quinns Island sediment transect concentrations (Table 7.28). More importantly, the DPOC:TPOC ratio in May 1980 did not markedly vary from the other water-column ratios or from the tidal flat sediment ratios.

There were observable differences among the five intensive benthic study sites and the transects within the sites (Table 7.28). Clatsop Spit had the lowest mean DPOC concentration of the five sites, but the highest DPOC:TPOC ratio; thus, even though detrital carbon concentration was low, it made up almost the entire content of the total carbon concentration. At the other four sites, the marsh transect registered the highest DPOC concentrations. The upper intertidal transect usually had the lowest DPOC concentrations of the three transects at each sampling site, and the lowest DPOC:TPOC ratios; thus, the upper transect usually had the highest relative concentrations of living biomass. The Youngs Bay site had the lowest mean DPOC:TPOC ratio over all transects, indicating that Youngs Bay had the highest living biomass concentration relative to total particulate organic carbon.

Vascular Plants

The annual detrital biomass from the emergent marsh vegetation can be estimated roughly as the difference between total annual above-ground production and loss due to grazing. If grazing is assumed to be minimal, then net annual detritus production would approximately equal net annual primary production. There were 11,324 MT C yr^{-1} produced as above-ground vegetation in the high and low marshes of the Columbia

Table 7.27. Concentrations of detrital particulate organic carbon (DPOC) and DPOC as a fraction of total particulate organic carbon (TPOC) in regions 8, 7, 3 + 5 and 1 of the Columbia River Estuary.

Month	DPOC (mgC m^{-3})				DPOC:TPOC			
	Region 8	Region 7	Region 3+5	Region 1	Region 8	Region 7	Region 3+5	Region 1
February	595	633	683	759	0.73	0.77	0.84	0.93
April	632	655	686	748	0.69	0.72	0.77	0.82
May	4,781	4,948	5,060	5,214	0.88	0.89	0.92	0.94
July	674	684	957	968	0.58	0.60	0.82	0.82
September	1,098	1,125	1,260	1,309	0.77	0.82	0.90	0.96
November	1,327	1,342	1,405	1,425	0.86	0.89	0.93	0.95

Table 7.28. Detrital particulate organic carbon (DPOC) in the top centimeter of sediment for the five intensive study sites, and for the transects within each intensive study site. Values are annual means.

	DPOC($gC\ m^{-2}$)	DPOC:TPOC
Clatsop Spit	29.8	0.96
Upper (0.7 m above MLLW)	27.4	0.87
Lower (0.3 m above MLLW)	32.4	0.96
Youngs Bay	76.2	0.78
Marsh (0.9 m above MLLW)	90.0	0.80
Upper (0.7 m above MLLW)	70.7	0.74
Lower (0.3 m above MLLW)	67.0	0.79
Baker Bay	104.9	0.85
Marsh (0.9 m above MLLW)	127.0	0.86
Upper (0.7 m above MLLW)	88.7	0.79
Lower (0.3 m above MLLW)	98.3	0.89
Grays Bay	87.5	0.89
Marsh (0.9 m above MLLW)	99.6	0.90
Upper (0.7 m above MLLW)	75.8	0.89
Lower (0.3 m above MLLW)	87.1	0.89
Quinns Island	66.8	0.89
Marsh (0.9 m above MLLW)	109.7	0.89
Upper (0.7 m above MLLW)	39.0	0.83
Lower (0.3 m above MLLW)	50.0	0.93

River Estuary (see Chapter 8). Assuming that 53% of this production was either grazed away or translocated into rootstocks by fall (see Section 7.1.7), then 47% of the annual production, about 5,320 MT C yr^{-1}, became detritus. If all of this detritus were evenly distributed over the high and low marsh in early winter, the concentration would be about 150 gC m^{-2}. However, the distribution certainly was not uniform. There was no one representative concentration of emergent plant detritus for the Columbia River Estuary, just as there was no single representative concentration for water-column detritus (Table 7.27) or tidal flat detritus (Table 7.28).

7.2.3 Resource Inputs and Controlling Physical Processes

Nutrient Input

No data were available relative to the effect of nutrient supply on the living bacteria and fungi in the detrital biomass.

Temperature

Temperature controls rates of decomposition and other detritus-associated rates in the same way it controls production rates; i.e., each 10°C rise in temperature within microbial tolerance limits should elicit an approximate doubling in decomposition rate. From temperature distributions in the estuary (see Chapter 3) it might be expected that detritus should decompose about twice as fast in summer as in winter, but no data are available.

Mechanical Reduction of Large Particles

It would be expected that shredding, cutting, grinding, and other means of reducing large detrital fragments to small particles would greatly accelerate the decomposition process. Whether such fragmentation is done by animals during the process of feeding, or by physical means such as wave action, currents and tidal movements, the result is a mechanical reduction of large particles to small ones.

Large detrital fragments of primary biomass in the Columbia River Estuary were derived mainly from marsh plant litter. This litter was both mechanically and biochemically reduced to smaller and smaller particles with time. Results from litter bag experiments in low and high marsh and in brackish and freshwater regions of the Columbia River Estuary showed that there was a 0.33% mean daily loss of dry weight (Macdonald and Winfield, 1984). However, there was a general pattern of more rapid decomposition over the first 60 days of the experiments, and a slower rate thereafter. Losses in brackishwater marshes ranged from 0.19 to 0.44% day^{-1}, while losses in freshwater marshes ranged from 0.21 to 0.44% day^{-1}. Even though these rates of loss were very similar, after about 200 days the percentage dry weight remaining in brackishwater litter averaged 38.5%, while the percentage remaining in freshwater litter dropped to 10.8%. Decomposition obviously was accomplished somewhat faster in fresh water than in brackish water. Fragmentation and decomposition in air was much slower than in water.

Even at the most rapid rate of fragmentation and decay, some small amount of refractory material will not be degraded before the onset of the next growing season. Unless that material is swept from the marshes and either deposited on the estuary bottom or carried out to sea it will collect for long periods in the marshes.

No studies comparable to litter bag studies have been performed to investigate the combined mechanical and chemical decomposition of dead animal carcasses, molted exoskeletons, and fecal matter.

Biochemical Decomposition

As indicated above, the process of biochemical decomposition itself occurs simultaneously with the various processes of mechanical fragmentation. No independent, unequivocal measurements of aerobic or anaerobic biochemical decomposition of detrital particles were made for the Columbia River Estuary, so decomposition rates were unknown. Furthermore, inclusion of the biomasses of living microheterotrophs with the non-living detrital mass meant that growth of microheterotrophs was taking place at the same time as decomposition of non-living detrital particles. Part of the detrital decomposition process as defined herein was thus simply a transfer of organic matter from the dead organic pool to live micro-organism tissue.

7.2.4 Process-Generated Outputs

The release of dissolved organic matter (DOM) through aerobic or anaerobic decomposition in the Columbia River Estuary is probably mainly microheterotroph-mediated conversion of particulate detritus to dissolved compounds. No measure of this conversion was made for the Columbia River Estuary. Presumably if the numbers of living heterotrophs associated with non-living detrital particles increased, the amount of DOM released into the water would increase. The respiratory and anaerobic metabolic activity also would increase, and therefore the non-living detrital mass would disappear faster. Decomposition thus generates two types of outputs: 1) dissolved organic matter, some of which can be reutilized by micro-organisms very quickly and some of which is either buried with sediments, released to the air, or requires further breakdown before *in situ* use; and 2) dissolved gases, one of which (carbon dioxide) is the end product of aerobic respiration and oxidative metabolism.

Detrital respiration (actually respiration of the microheterotroph component of detritus) in the water column and in rafts and windrows of dead emergent plants was not measured directly. However, detrital respiration for the five intensive study sites in the tidal flats was calculated as the difference between total benthic community respiration and respiration due to benthic autotrophs (HR in Table 7.17). These detrital respiration estimates might have included some chemical oxidation as well as microfloral and microfaunal metabolism. Nevertheless, the detrital respiratory rate in Youngs Bay, at 0.014 gC m^{-2} day^{-1}, was by far the lowest, while the detrital respiratory rate in Baker Bay was the highest. However, the ratio of detrital respiration to total benthic respiration (HR:OCON) was quite uniform in Baker Bay, Grays Bay, and Quinns Island (0.456, 0.429, and 0.446, respectively). In Youngs Bay, HR:OCON was very low (0.023), indicating a basically autotrophic respiration rather than heterotrophic or detrital. Conversely, HR:OCON was high (0.779) at the Clatsop Spit site, signifying a predominately heterotrophic respiration.

7.2.5 Non-Process Generated Inputs and Outputs

Natural Mortality, Fecal Production and Detrital Consumption

Deaths of phytoplankton, benthic algae, vascular plants, and estuarine vertebrates and invertebrates are all considered inputs to the detrital pool. Mortality rates are seldom known, however, so that the rate of conversion of living organic matter to non-living detritus is seldom known. Non-grazing losses from living phytoplankton biomass are partly due to death and sinking of phytoplankton cells, but also are partly due to process-generated outputs such as respiratory losses and excretion of dissolved organic matter. The estimated rates of natural mortality of phytoplankton in the Columbia River Estuary are given in Table 7.21. No estimates of benthic algal mortality were available for the Columbia River Estuary. The best estimate of vascular plant mortality was the fall die-off in the marshes after losses due to consumption and translocation were accounted for (5,320 MT C yr^{-1}); however, any small die-offs during the growing season were not evaluated, and would not even have been detected if the dead material disintegrated or was swept away between sampling periods.

No data on natural mortality of invertebrate animals were available for the Columbia River Estuary, yet a great contribution must have come from the death and decomposition of zooplankton, benthic infauna and epibenthic organisms. Even though much of the invertebrate biomass must be eaten each year, a substantial quantity of invertebrate biomass must enter the detrital pool directly through natural mortality. This contribution was unknown for the Columbia River Estuary.

Fish, seals, small furbearers, reptiles, amphibians, and estuarine birds all must have contributed to some degree through natural mortality to the detrital pool in the estuary. Natural mortality estimates for mobile vertebrate populations are exceedingly hard to make, but the annual detrital contribution from combined vertebrate deaths was probably small compared to contributions of plant and invertebrate biomasses. To illustrate, the maximum natural mortality contribution of muskrat was estimated from data gathered by Merker and Fenton (1984), and was then compared with the phytoplankton contribution to the detrital pool. Maximum muskrat mortality from natural mortality and predation was calculated as 2.6 MT C yr^{-1}. Assuming 10% of this total mortality was attributed to natural mortality, then natural mortality was 0.26 MT C yr^{-1}. Rough conversion of phytoplankton areal mortality rates (Table 7.21) to annual estuary-wide rates yielded about 47,140 MT C yr^{-1}, an enormously greater detrital input than muskrat carcasses. The maximum addition of nutria carbon to the long-term detrital pool via natural mortality was calculated as 2.53 MT C yr^{-1}, larger by an order of magnitude than the muskrat contribution because of greater size of nutria, and greater numbers in the estuary. The nutria contribution was still small relative to the phytoplankton input to the detrital pool, however. Fish carcasses undoubtedly contributed to the detrital pool, though the major loss of fish biomass in the estuary was still likely to be from live predation and rapid scavenging of recently dead individuals. Unfortunately no estimates of consumption of detritus by any animal group were available, so this potentially substantial output from the detrital pool remained unevaluated.

A potentially large annual contribution to the detrital pool was from cast exoskeletons of invertebrates and from fecal deposition by all animals. No molting rates or fecal deposition rates were measured for organisms in the Columbia River Estuary. However, some measure of significance was obtained by calculating approximate fecal deposition rates using muskrat, again, as an example. Merker and Fenton (1984) assumed muskrats of all ages and both sexes consumed one-third of their body weight per day. Making computations on the basis of maximum numbers and individual weights of kits and adults, maximum ingestion was estimated to be 4,454.8 MT fresh food yr^{-1} in the Columbia River Estuary (Merker and Fenton 1984). Because the food items of muskrat are mostly herbaceous plants and their rootstocks, assimilation was likely to be about 70% of ingestion; therefore, egestion of fecal matter was approximately 30% of ingestion, or 1,336 MT fresh weight yr^{-1}. If carbon content is about 10% of fresh weight, then muskrat fecal material contributed approximately 133.6 MT C yr^{-1} to the detrital pool. This was a substantially greater input than muskrat carcasses, and about 0.3% of the phytoplankton input. Making the same calculations with nutria, using maximum population estimates (Merker and Fenton 1984), 991.9 MT C yr^{-1} was put into the detrital pool as nutria fecal matter. This was 2.1% of the phytoplankton natural mortality input. Fecal deposition by all invertebrates and vertebrates must have represented a relatively large fraction of the total annual detrital input to the estuary.

Import and Export of Detritus

Import of suspended detrital particles from the Columbia River and transport through the estuary was calculated in an identical manner to the calculation of PPOC import, using appropriate exchange rate data from Table 7.22 and DPOC concentrations from Table 7.27. Transports of DPOC for regions 8, 7, 3 + 5 and 1 are given in Table 7.29 for the months sampled. In February and April the detrital transport first increased slightly from region 8 to region 7, then decreased in regions 3 + 5. In May, September and November, transport increased from region 8 through regions 3 + 5, with the increase somewhat greater between regions 7 and 3 + 5 than between regions 8 and 7. In July a striking increase in detrital transport in regions 3 + 5 was observed. In July, and to a lesser extent in May, September and November, living phytoplankton was transformed to detrital carbon in the study area, and/or detrital carbon was brought into the estuary from sources other than from upriver. Mechanisms that could have been responsible for the enhanced transports in regions 3 + 5 included 1) resuspension of bottom particulates into the estuarine water column, 2) conversion of living freshwater phytoplankton to detrital carbon at brackishwater interfaces, and 3) increased production and suspension of fecal particulates in the estuarine water column. The decrease in detrital transports between regions 7 and 3 + 5 in February and April were the result of large mixing terms and much larger detrital concentrations in the Entrance Region (region 1) than in the mixing zone (regions 3 + 5).

Annual import of suspended detrital carbon from the Columbia River into the study area, without the Mount St. Helens load considered, was estimated at 146,495 MT. With the volcanic load, the annual import was about 268,725 MT C. Comparable transport to the Entrance Region was estimated at 159,185 MT C yr^{-1} without the volcanic addition, and 285,635 MT C yr^{-1} including the volcanic debris. A net increase of detrital carbon in the estuary was estimated as the difference, or 12,690 MT yr^{-1} without the volcano effect, and 16,910 MT yr^{-1} with the volcano effect.

Besides the 146,495 MT C yr^{-1} that entered the estuary directly from the Columbia River as suspended DPOC (not considering the volcanic load), about 47,140 MT C yr^{-1} presumably was generated in the estuary from natural mortality of living phytoplankton (calculated from Table 7.21). Of the 17,155 MT yr^{-1} of living phytoplankton carbon produced in the estuary (see Chapter 8) plus an estimated 56,261 MT yr^{-1} of living phytoplankton carbon imported from upriver (from Table 7.23), only 34,345 MT yr^{-1} was estimated to be exported into region 1 (from Table 7.23). The difference between the living phytoplankton carbon in the estuary and that exported into region 1, or about 39,070 MT yr^{-1}, was presumed to be converted to detrital particles, mostly at the freshwater-brackishwater interface. The 39,070 MT C yr^{-1} calculated as above compared reasonably to the 47,140 MT C yr^{-1} calculated from natural mortality rates in Table 7.21. In addition, a major portion of the annual emergent marsh plant production of 11,324 MT C yr^{-1} (see Chapter 8) was presumed to die back each year and enter the detrital pool of the estuary. The fraction of benthic algal production of the tidal flats that entered the detrital pool was not known; however, because total annual production was relatively small, the fractional contribution to detritus would also be small.

The sum of direct detrital carbon import to the estuary (146,495 MT yr^{-1}) plus estimated phytoplankton-derived generation in the estuary (39,070 MT yr^{-1}) plus a presumed direct detrital carbon input from emergent marsh vegetation equivalent to 47% of above-ground production (about 5,320 MT yr^{-1}) equals 190,885 MT yr^{-1} of detrital carbon with the potential to be exported through the Entrance Region. The estimated transport of suspended particulate organic detrital carbon into region 1 was approximately 159,185 MT yr^{-1}. Thus, the difference between the potential export and the estimated export, or 31,700 MT C yr^{-1}, was the best estimate of detrital carbon remaining in the estuary. This remaining carbon likely was distributed in the marshes as large, refractory pieces of emergent vegetation and on the estuary bottom as more finely divided material. If any detrital material was swept out of the estuary along the bottom rather than suspended in the water column, it was not estimated; thus, export into region 1 could be greater than the estimated value if such near-bottom export occurred. Also, any input from benthic algal production and animal production to the detrital pool would alter the estimates of detrital export and retention. Finally, any dredging activity would also have an impact on detrital carbon remaining in the estuary each year.

Table 7.29. Daily transport of suspended detrital carbon through regions of the Columbia River Estuary, for each sampling month.

Month	Transport Rates (MT C day^{-1})		
	Region 8	Region 7	Regions 3 + 5
February	440.3	468.4	405.1
April	502.4	520.6	516.1
May	4,419.9	4,574.3	4,593.5
July	349.4	354.6	492.2
September	256.1	262.4	286.1
November	458.6	463.8	481.1

7.3 CONSUMPTION PROCESSES

7.3.1 Introduction

Consumption processes involve animals eating plants and other animals and are defined literally as the processes by which animals "destroy or burn" plants and other animals for their energy content. While primary production processes (including those importing live and dead organic matter into the estuary) ultimately determine the carrying capacity of the estuarine biota, consumption processes typically determine the structure of the estuarine communities. Consumers are also the foci of human interactions with the estuarine ecosystem, not only because they are often more visible than many of the primary producers but also because they are commercially or recreationally important, aesthetically appreciated, and/or because they structure the community through selective predation pressure. Understanding the influences upon consumer occurrence, distribution, and abundance is, however, a complicated undertaking because both physical (e.g., circulation, salinity regime) and biotic (e.g., distribution and standing stock of food resources) attributes and processes are synergistically related. The conceptual model (Chapter 6) attempts to identify some of these relationships.

Model and Couplings

Organic matter produced by the Primary Food Processes subsystem is transferred to consumer organisms through the Consumption Processes subsystem (Figure 6.8). Three basic processes are involved in changing the state of organic matter within the Consumption Processes subsystem: ingestion, defecation, and excretion. Initially within the Consumers State Variable, this transfer of organic matter couples directly with primary consumers and is subsequently transferred progressively up the food web through secondary and tertiary consumers. Thus, although at the Consumption Processes subsystem level Consumers comprise the only state variable, this category is functionally divided into primary and higher level consumers. As a result, within the subsystem there are also two changes of state: (1) life history changes of organisms from one consumer category to the other (normally from primary consumer to secondary consumer); and (2) consumption of lower (i.e., primary and secondary) by higher (i.e., secondary and tertiary, respectively) level consumers. An expansion of the Consumption Processes subsystem indicates four subsystems (Figure 6.2), three of which (Wetland Herbivory, Deposit Feeding, and Suspension Feeding) involve primary consumer animals (Figures 6.9-6.11) and one of which (Predation) involves all consumption processes above the primary or "grazing" level (Figure 6.12).

The four subsystems basically define metazoan feeding modes or strategies. Wetland Herbivory describes the processes by which terrestrial and aquatic organisms feed (often termed "graze") upon living plants in wetland habitats of the estuary; in this case, plants are confined to macrophytes as opposed to microphytes utilized by protozoans. Deposit Feeding describes the microphagous feeding mode in which organisms process (by a variety of mechanisms) sediments and associated detritus, selectively removing or digesting both living and non-living organic particles. Suspension Feeding, on the other hand, describes macrophagous feeding upon food particles suspended in the water, typically through some form of mechanical filtering mechanism or apparatus such as gills. Predation is simply the process of carnivorous feeding by higher level (secondary and tertiary) consumers upon lower level (primary and secondary) consumers; predators which may also scavenge dead animal tissue have been included within Predation.

Primary Food Supply, which constitutes the only state variable resource input to the Consumption subsystem, includes two food sources in the form of (1) Primary Production Processes, i.e., "live", autotrophically produced organic matter, and (2) Detrital Decomposition Processes, i.e., the diverse array of non-living organic debris particles collectively called "detritus". Although detritus has been termed "dead" organic matter, typically it is highly enriched by a very "live" community of microflora and microfauna in the form of viruses, bacteria, fungi, and protozoans which are linked in a "microbial loop" along with nutrients (nitrogen and phosphorus), dissolved organic matter (DOM), particulate organic matter (POM), and minerals (Fenchel and Jorgensen 1977; Azam et al. 1983).

There are many factors affecting or regulating consumption processes, which vary widely as a function of the particular ingestion characteristics of the various state variables (organisms) within the four subsystems. Physical variables include principally light intensity, water turbidity, water velocities, and temperature. Biological variables involve the distribution and abundance of food particles and organisms, behavioral responses of prey, competitive interactions with other consumers, and selective predation upon the consumers in question.

As in the Primary Food Processes subsystem, process-generated outputs include respiratory losses of CO_2 and release of DOM; energy is also lost in the form of heat generated by consumption processes but is not accounted for in this material approach. A third output involves the loss of POM to the detritus resource (state variable) through the production of feces and wastage from the ingestion process. Although not shown explicitly in Figure 6.8, some of these products of the consumption process may also cycle back to the Primary Production subsystem as nutrients in the form of respiratory CO_2 and DOM.

Other couplings at the Consumption Processes subsystem level involve the transport of living organisms and other states of organic matter not generated by consumption processes into, out of, and within the subsystem. Contributions of exuvia (animal molts) and non-living organisms or parts thereof to the detritus resource encompass the principal form of non-process-generated transfer out of the subsystem. When the Consumption Processes subsystem is considered on a spatial scale, such transfers also encompass immigration (import) and emigration (export) of living consumers across the subsystem boundaries.

Thus, in terms of accounting for biomass (herein usually measured in units of carbon [C]) changes through the Consumption Processes, consumption must equal the sum of production, respiration, and excretion. Production can be further partitioned into growth and reproduction and excretion into the processes producing egesta and excreta.

Database

Data from seven categories of consumers (wildlife, benthic infauna, epibenthic organisms, zooplankton and larval fish, fish, avifauna, marine mammals) were obtained minimally on a seasonal basis (i.e., avifauna) and maximally on a bi-monthly basis (i.e., zooplankton and larval fishes). Sampling of consumers occurred at various locations throughout the estuary and was often systematically stratified by salinity zone and general habitat (defined by depth, sediment structure, emergent vegetation, etc.). In a few cases, mutual study sites (designated the "intensive study sites") were occupied by investigators from several work units, including all those studying primary production processes and several (benthic infauna, epibenthic organisms) studying secondary consumers, although sampling times did not often coincide. Consumers such as avifauna and terrestrial, aquatic, and marine mammals were generally sampled using non-destructive techniques such as transect surveys or plot censuses. Most of the other consumer assemblages were typically sampled using destructive methods (i.e., without replacement except in cases of extremely large collections, which were systematically subsampled) in which the organisms were removed from the environment and retained for identification, enumeration, weighing, measuring, and other processing.

Data acquisition was quantitative. Abundance and biomass of organisms were measured per standardized unit of sampling effort, allowing conversion of state variables (e.g., density, standing crop) and processes (e.g., consumption rate) to an areal (m^{-2}) basis which could subsequently be expanded by sampling strata (e.g., estuarine habitat, zone, or region). Table 7.30 briefly summarizes the sampling designs, methodologies, and data characteristics for the CREDDP investigations of consumer organisms. In some cases data were aggregated according to the hydrology seasons described in Section 2.2.4.

7.3.2 Taxonomic Structure and Organization of Consumer Assemblages

Discussion of the taxonomic structure and organization of consumer organism assemblages is organized according to the four process divisions of the Consumption subsystem. Wherever possible, the taxa have been condensed into functional groups, either subjectively or quantitatively via numerical classification or other multivariate analyses. The resulting groups are then treated as unit populations of consumers if justified by common feeding modes among the group taxa.

Wetland Herbivory

Among the avian species studied in the estuary, two dabbling ducks - mallard (*Anser platyrhynchos*) and American wigeon (*Mareca americana*) - and the black-capped chickadee (*Parus atricapillus*) were

Table 7.30. Sampling design, methods used, and variables measured by CREDDP investigations of consumer organisms in the Columbia River Estuary, 1979-1981.

CONSUMER TAXA	FEEDING CATEGORY	TIME PERIOD	
BENTHIC INFAUNA	Deposit & suspension feeders;	August 1980-September 1981	Sampling Design Vertical distribution at three sites; monthly to biweekly production at one littoral flat; *Corophium* life history and monthly changes in infauna at two tidal flats; distribution over whole estuary relative to 16 salinity and substrate depth strata. Methods Three 30 cm deep 20.3 cm cores sieved between 4.0- and 0.063 mm mesh screens; five 10.2cm cores to 10 cm depth sieved to 0.125 mm; 200 0.05 m^2ponar grab samples. Variables Measured Species composition, density, standing crop m^{-2}; life history and production of *Corophium salmonis*.
EPIBENTHIC ZOOPLANKTON AND MOTILE MACRO-INVERTEBRATES	Deposit & suspension feeders; predators	March 1980-August 1981	Sampling Design Monthly to Quarterly sampling at 16 sites stratified by three habitats and four estuarine zones. Methods Duplicated samples w/0.1 m^2 epibenthic pump w/0.500-, 0.253-, and 0.130 mm mesh nets; 0.5 m epibenthic sled w/ two 0.130 mm nets 37 m beach seine; 4.9m semi-balloon trawl. Variables Measured Occurrence, density standing crop, m^{-2} and m^{-3}; macroinvertebrate length and % occurrence, abundance, & biomass of stomach contents.

Table 7.30. (Continued)

CONSUMER TAXA	FEEDING CATEGORY	TIME PERIOD	
PELAGIC ZOOPLANKTON AND LARVAL FISH	Suspension feeders; predators	April 1980-September 1980	Sampling Design Bi-monthly distribution at 10 stations along length of mid-channel from RM-5 to RM-23. Methods 5-min double-oblique tow of double 0.2 m^2 net sled w/0.253 and 0.355 mm mesh. Variables Measured Occurrence and density m^{-2}; measurements.
FISH	Predators	February 1980-July 1981	Sampling Design Monthly sampling at 22 trawl, 16 purse seine, 11 beach seine and 14 trapnet sites; diel sampling at one. Methods 8-m semi-balloon trawl; 200m purse seine; 50mm beach seine; trapnets. Variables Measured Occurrence, density and standing crop m^{-2}; occurrence, abundance, biomass of stomach contents; lengths.
AVIFAUNA	Herbivores; Predators	April 1980-March 1981	Sampling Design Monthly or more frequent sampling of 72 0.8 to 5 km transects; variable circular plots; incidental sitings. Methods Transects and plot observations; behavioral. Variables Measured Occurrence and abundance 40.5 ha or km^{-1}, assemblage diversity.

Table 7.30. (Continued)

CONSUMER TAXA	FEEDING CATEGORY	TIME PERIOD	
TERRESTRIAL & AQUATIC by MAMMALS	Herbivores; Predators	April 1980-May 1981	Sampling Design 27-150 m^2 land and boat transects stratified wetland habitat. Methods Transect observations; small mammal traps; radiotelemetry; scat, stomach analysis. Variables Measured Occurrence, abundance, feeding sites ha^{-1};% frequency occurrence and composition of food items.
MARINE MAMMALS	Predators	March 1980-September 1981	Sampling Design Weekly to monthly monitoring of population within and adjacent to estuary relative to species/life history composition, distribution, and behavior. Methods Aerial surveys of haulout sites; examination of stranded and recovered specimens; mark and recapture; radiotagging; scat, stomach analysis. Variables Measured Occurrence & abundance overall; % occurrence of prey items; population turnover via emigration and immigration.

the prominent wetland herbivores. Mallards were distributed principally in peripheral bays and in the islands of Cathlamet Bay, with the greatest occurrences in the vicinity of Long and Karlson Islands during spring and fall migration periods (Figure 7.28a). While mallards were considered characteristic of open water (bay), tidal flat, and marsh habitats, consumption of emergent vascular plants occurred primarily in marshes and occasionally on the tidal flats. Although less common, American wigeon occurred during the same seasons in approximately the same regions and habitats (Figure 7.28b). While they were more characteristic of shrubby and wooded estuarine habitats, black-capped chickadees were also found in the marsh and island habitats of Cathlamet Bay and the Fluvial Region.

Nutria or coypu (Myocastor coypus), muskrat (Ondatra zibethica), American beaver (Castor canadensis), Columbian white-tailed deer (Odocoileus virginianus leucurus), black-tailed deer (O. hemionus columbianus), deer mouse (Peromyscus maniculatus), and Townsend's vole (Microtus townsendii) constituted the mammalian wetland herbivores among the ten species studied by Dunn et al. (1984). Nutria, muskrat, and beaver were distributed in marsh and swamp habitats bordering all peripheral bays and throughout the islands of the Cathlamet Bay and Fluvial Regions (Figure 7.29). Despite the apparent overlap in the distributions of these three species, detailed enumeration of feeding sites indicated that grazing per se was more localized in specific emergent plant assemblages (Merker and Fenton 1984). Nutria and muskrat feeding sites were most common in reed canary grass/cat-tail, Lyngby's sedge/horsetail, and colonizing soft-stem bulrush habitats, although to contrasting degrees, while the Sitka spruce and Sitka willow habitats were the most important beaver feeding habitats. Black-tailed deer were observed principally in the marsh habitats in the lower reaches of the estuary (Baker, Trestle, and Youngs Bays), while Columbian white-tailed deer were restricted to the islands of Cathlamet Bay and the Fluvial Region (Figure 7.30). Along the margin of tidal flat habitats, deer appeared to be feeding most often in the reed canary grass/cat-tail and Sitka willow habitats. Small terrestrial mammals, including the deer mouse and Townsend's vole, were widespread in wetland habitats throughout the estuary and appeared to commonly utilize forage plant matter from both swamp and marsh habitats. Itemization of the feeding sites of the Townsend's vole indicated that both short and tall Lyngby's sedge habitats appeared to support most of their grazing pressure.

Deposit Feeding

In contrast to the well-studied rocky intertidal and shallow subtidal communities of the Pacific Northwest coast, which are typically dominated by suspension feeders (see Carefoot 1977 for synopsis), benthic infaunal and epifaunal assemblages of the region's coastal estuaries appear to be dominated by deposit feeders (see reviews by Simenstad, in press, and Simenstad and Armstrong in prep.). This is particularly true of benthic infauna assemblages in the Columbia River Estuary, in which suspension feeders are comparatively rare to non-existent components (Table 8.4).

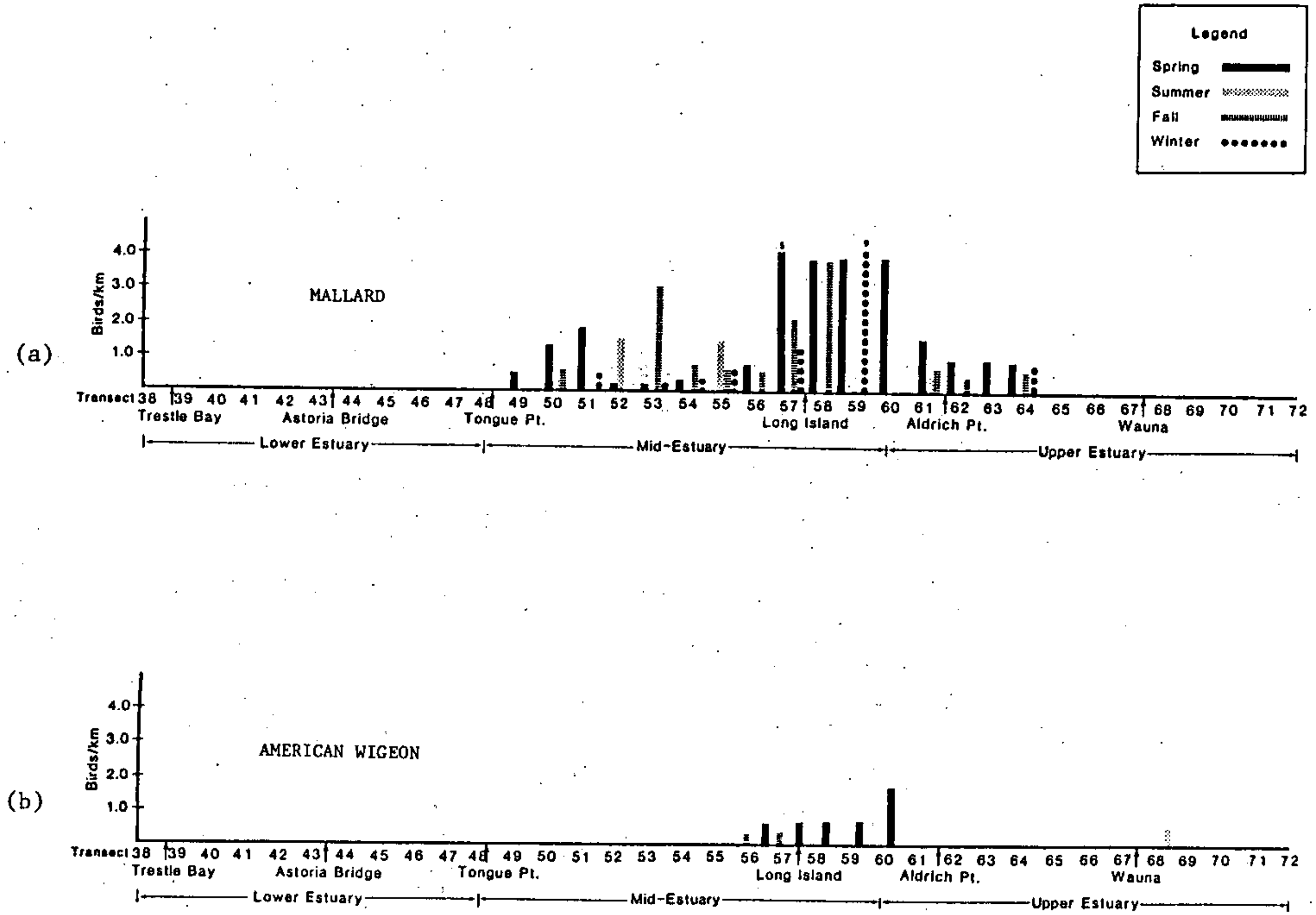


Figure 7.28. Distribution and relative abundance (birds/km) of mallards (a) and American wigeons (b) during 1980 and 1981 (Hazel et al. 1984).

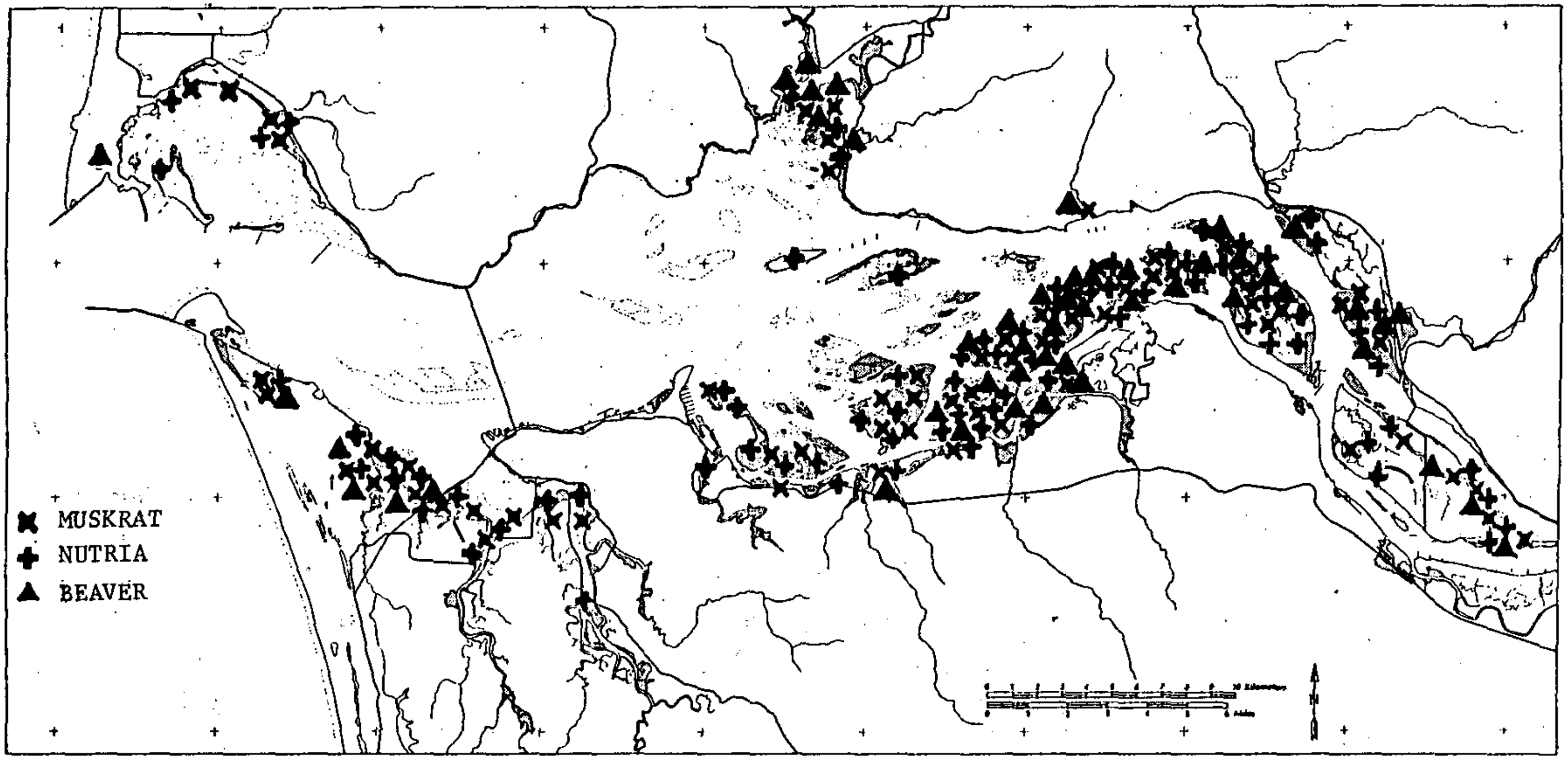


Figure 7.29. Distribution of herbivorous aquatic mammals utilizing wetland habitats of the Columbia River Estuary during CREDDP studies, 1980-1981. Symbols indicating locations of muskrat, nutria, and beaver observations are representational; see Dunn et al. (1984) for more exact locations.

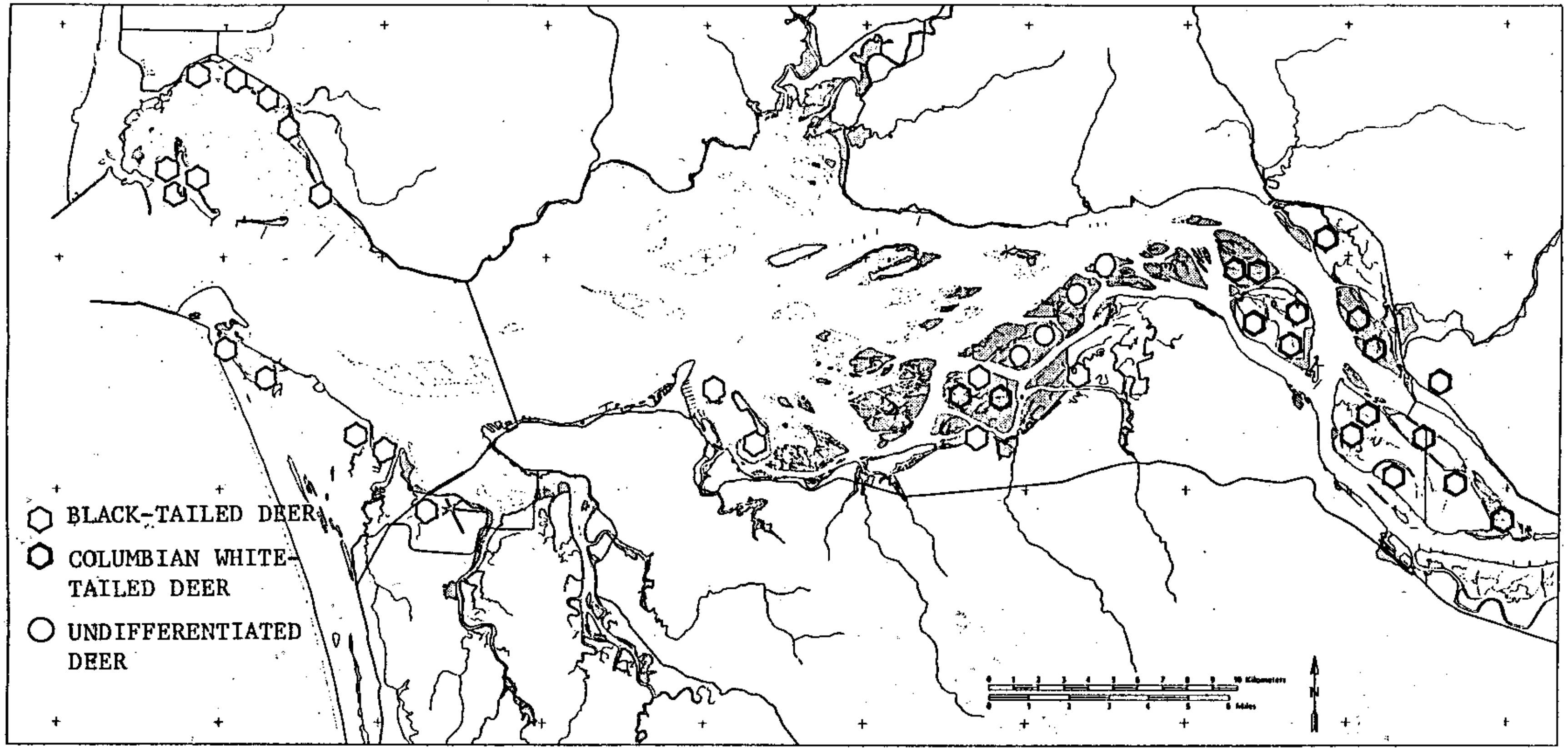


Figure 7.30. Distribution of herbivorous terrestrial mammals utilizing wetland habitats of the Columbia River Estuary during CREDDP studies, 1980-1981. Symbols indicating locations of deer observations are representational; see Dunn et al. (1984) for more exact locations.

Benthic Infauna

Prominent (either numerically or gravimetrically) deposit feeders in the estuary's benthic infauna assemblages include bivalves (*Macoma balthica*), oligochaetes, polychaetes (*Hobsonia florida*, *Neanthes limnicola*, *Fluminicola virens*, and *Goniobasis plicifera*), and amphipods (*Corophium salmonis*, *Paraphoxus milleri*, *Eohaustorius estuarius*). Other, less prominent deposit feeders include the polychaetes *Pseudopolydora kempi*, *Paraonella platybranchia*, *Spio* spp., *Polydora ligni*, *Pygospio elegans*, and *Mediomastus* spp.

Reciprocal averaging ordination of density data from the distributional survey of benthic infauna indicated associations among deposit-feeding benthic infauna along environmental gradients and the distribution of these associations among discrete habitats (Holton et al. 1984). Four basic infaunal invertebrate assemblages were identified to be associated with particular habitats and zones of the estuary (Table 7.31). Although several suspension feeders were also important in defining these assemblages (e.g., *Corbicula manilensis*), almost all of the principal and secondary taxa in the four assemblages were deposit feeders. The positions of these assemblages were subjectively outlined relative to the distribution survey station scores along the two most important reciprocal averaging axes (i.e., salinity and sediment texture; Figure 7.31). This plot illustrates that an assemblage defined primarily by the abundance of the tubiferous amphipod *Corophium salmonis* is almost completely confined to the tidal-fluvial zone in the estuary, although the group is homogeneously distributed across many habitats (substrate types) within this zone. The second assemblage comprised the dominant taxa in the relatively protected tidal flats of Baker Bay and essentially the complete assemblage in the same habitat at Youngs Bay. The third assemblage, characterized by the gammarid amphipod *Eohaustorius estuarius* and the polychaete *Neanthes limnicola*, originated exclusively from mainstem and minor channel stations in the estuarine mixing zone. The fourth assemblage, also defined by amphipods and polychaetes, was prevalent in more coarse-grained channel and exposed tidal flat habitats in the plume and ocean and estuarine mixing zones.

Epibenthic Zooplankton

Assemblages of epibenthic organisms which occupy the interface between the water column and bottom substrate are strongly influenced by both biological (e.g., demersal fish predation) and physical (e.g., boundary layer turbulence) processes but there are few explanations for their composition and maintenance (e.g., Hesthagen 1973; Sibert 1981). These assemblages are typically composed of micro-, meio-, and small macrofaunal crustaceans but larvae and other early life history stages of echinoderms, molluscs, and other marine taxa can also be prevalent (Bossanyi 1957). Unlike infauna, which have the relative protection allowed in occupying the sediment, these epifauna are relatively motile within the top 1 cm of the sediment surface (thus, the epibenthic "zooplankton" definition) and must be adapted to the rigors of life amid high current velocities, high concentrations of suspended sediments, low water visibility, shifting sediment structure, and concentrations of demersal fish and motile macroinvertebrate predators (see following

Table 7.31. Characteristic deposit feeding in four benthic infauna groups defined by reciprocal averaging ordination (from Holton et al. 1984).

GROUP NUMBER	CHARACTERISTIC TAXA	HABITAT/ZONE ASSOCIATION
1	Principal: *Corophium salmonis* Heleidae Chironomidae Oligochaeta Secondary: *Fluminicola virens* *Goniobasis plicifera* *Neanthes limnicola*	Exclusively tidal-fluvial zone habitats
2	Principal: *Hobsonia florida* *Macoma balthica* *Neanthes limnicola* Secondary: Oligochaeta Turbellaria *Pseudopolydora kempi*	Protected littoral flat in plume & ocean and estuarine mixing zones
3	Principal: *Eohaustorius estuarius* *Neanthes limnicola* Rhynchocoela	Channels and exposed littoral flats in estuarine mixing zone
4	Principal: Rhynchocoela *Paraphoxus milleri* Secondary: *Paraonella platybranchia* *Spio filicornis*	Exposed flats, mainstream channel, center and bottom, and minor channel in plume & ocean and estuarine mixing zones.

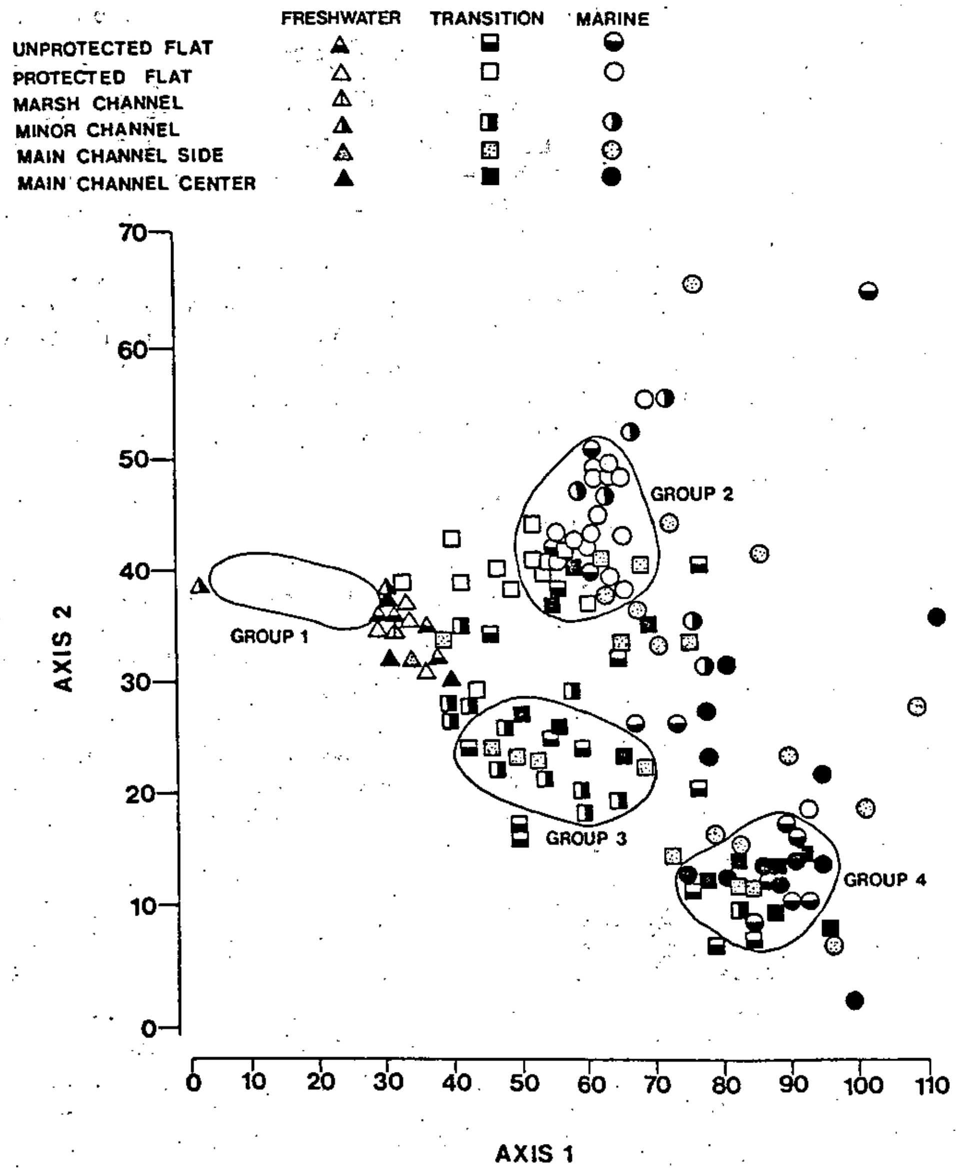


Figure 7.31. Results of reciprocal averaging ordination of benthic infauna data (Holton et al. 1984), expressed as a plot of station scores for the first two axes. Group designations are arbitrary, and are used to define probable animal assemblages. Group 1 is too densely packed for depiction of individual station points, but is composed entirely of freshwater zone stations. There were no obvious habitat groupings within Group 1. (See text for discussion of representative group taxa).

sections on Predators).

In the Columbia River Estuary, epibenthic zooplankton form a number of diverse assemblages of harpacticoid, calanoid, and cyclopoid copepods and gammarid amphipods (Simenstad 1984). Approximately 406 categories of epibenthic zooplankton taxa-life history stages were identified from tidal flat and demersal slope habitats and 292 categories were identified from channel bottom habitats (Simenstad 1984). The calanoid *Eurytemora affinis* was the most abundant species but harpacticoids (primarily an undescribed Ectinosomidae [*Ectinosoma* sp.?], *Scottolana canadensis*, *Microarthridion littorale*, *Tachidius triangularis*, and *Attheyella* sp.) comprised almost 35% of the mean density over the 18-month sampling period; *Cyclops* spp. were the most abundant cyclopoids (Table 7.32). Rotifers were also comparatively common and frequently abundant. Among these taxa, however, just the harpacticoid fauna should be considered predominantly deposit feeders upon epibenthic sediments, detritus, and associated microfauna and microflora (Heinle et al. 1977; Reiper 1978; Brown and Sibert 1977). As *Eurytemora affinis* apparently has the ability to utilize autotrophic (i.e., phytoplankton by suspension feeding) as well as heterotrophic (i.e., detritus by both suspension and deposit feeding) food resources (Heinle and Flemer 1975), we have assumed that they are both used principally by suspension feeding. The cladocerans and cyclopoids which are also common components of the estuary's epibenthic zooplankton assemblage are also assumed to be suspension feeders.

Numerical classification (hierarchical cluster analysis) of the epibenthic zooplankton density data indicated dramatic changes in station and taxa associations during the three hydrologic seasons (Chapter 2) (Figure 7.32a-c), similar to the dynamic structuring of fish assemblages during these periods (see following section). In May, during the high flow season, two station groups were evident, one within 25 km from the entrance of the estuary and one farther upriver (Figure 7.32a). Stations located in the tidal-fluvial zone were characterized almost entirely by a fluvial assemblage of suspension-feeding freshwater cyclopoids and cladocerans, although several deposit-feeding harpacticoid (*Tachidius*, *Attheyella*), ostracod (*Limnocythere*), and gammarid amphipod (*Corophium*) taxa also occurred in the tidal flat and demersal slope habitats of the upriver reaches of the estuary. Assemblages in the estuarine mixing and plume and ocean zones of the estuary were limited almost completely to euryhaline taxa, among which the deposit-feeding harpacticoids *Microarthridion* and *Bryocamptus* dominated one taxa group occurring in Baker Bay, and Ectinosomids, *Scottolana*, and *Parathatestris* were prominent in another taxa group characterizing the tidal flat and demersal slope habitats in the central regions of the estuary.

By October, at the end of the low flow season, assemblage structure had become much more complex (Figure 7.32b). Coincident with the increased mixing and salinity intrusion upriver during low riverine discharge, station associations were less robust and comprised as many as five cluster groups: (1) channel bottom habitats within 20 km of the entrance; (2) tidal flat and demersal slope habitats within 10 km of the entrance; (3) flats and slopes in the central regions of the estuary and a channel station 40 km from the entrance; (4) flats, slopes, and

Table 7.32. Numerical composition (%) of prominent (>1% of mean density) zooplankton taxa (class, family) among epifauna in the Columbia River Estuary, March 1980 - July 1981.

	Numerical Composition (%)			
	Neomysis mercedis		*Crangon franciscorum*	
Food Item	Estuary-wide Distribution June 1980 (n=54)	Seasonal Distribution Youngs Bay (n=26)	Estuary-wide Distribution August 1980 (n=41)	Seasonal Distribution Youngs Bay (n=39)
Diatoms	12.5	3.7	21.4	62.6
Nematodes	...	...	...	0.7
Rotifers	36.8	1.9	...	0.1
Polychaete Annelids; Nereidae	...	...	3.3	1.9
Cladocerans	0.4	0.6	0.6	0.1
Sida crystallina	0.4	...	...	...
Daphnia sp.	0.4	...	...	...
Bosmina sp.	17.6	5.0	0.6	0.4
Chydoridae	0.4			
Leydigia quadrangularis	0.4	...	...	...
Ostracods	1.1	...	0.1	...
Calanoid Copepods				
Eurytemora affinis	2.6	3.7	...	9.1
Harpacticoid Copepods	0.7	...	1.0	...
Scottolana canadensis	9.6	37.9	61.0	22.7
Ectinosomidae	3.3	41.6	1.0	1.3
Tachidiae	0.4	...	...	...
Tachidius triangularis	0.4	...	0.1	0.3
Cyclopoid Copepods	...	1.2	...	...
Cyclops sp.	1.1	...	...	...
C. bicuspidatus	1.1	1.9	3.7	...
C. vernalis	1.8	2.5	4.7	...
Barnacle cypris	...	...	1.0	...
Mysidacea	...	...	0.3	...
Gammarid Amphipods	1.1	...	...	...
Corophium sp.	...	...	...	0.3
C. salmonis	...	...	0.4	0.1
Eogammarus confervicolus	0.4	...	0.1	...
Eohaustorius sp.	0.1	...	...	...
Decapods				
Crangon franciscorum	...	...	0.6	0.1
Plant Detritus	0.4	...	...	...

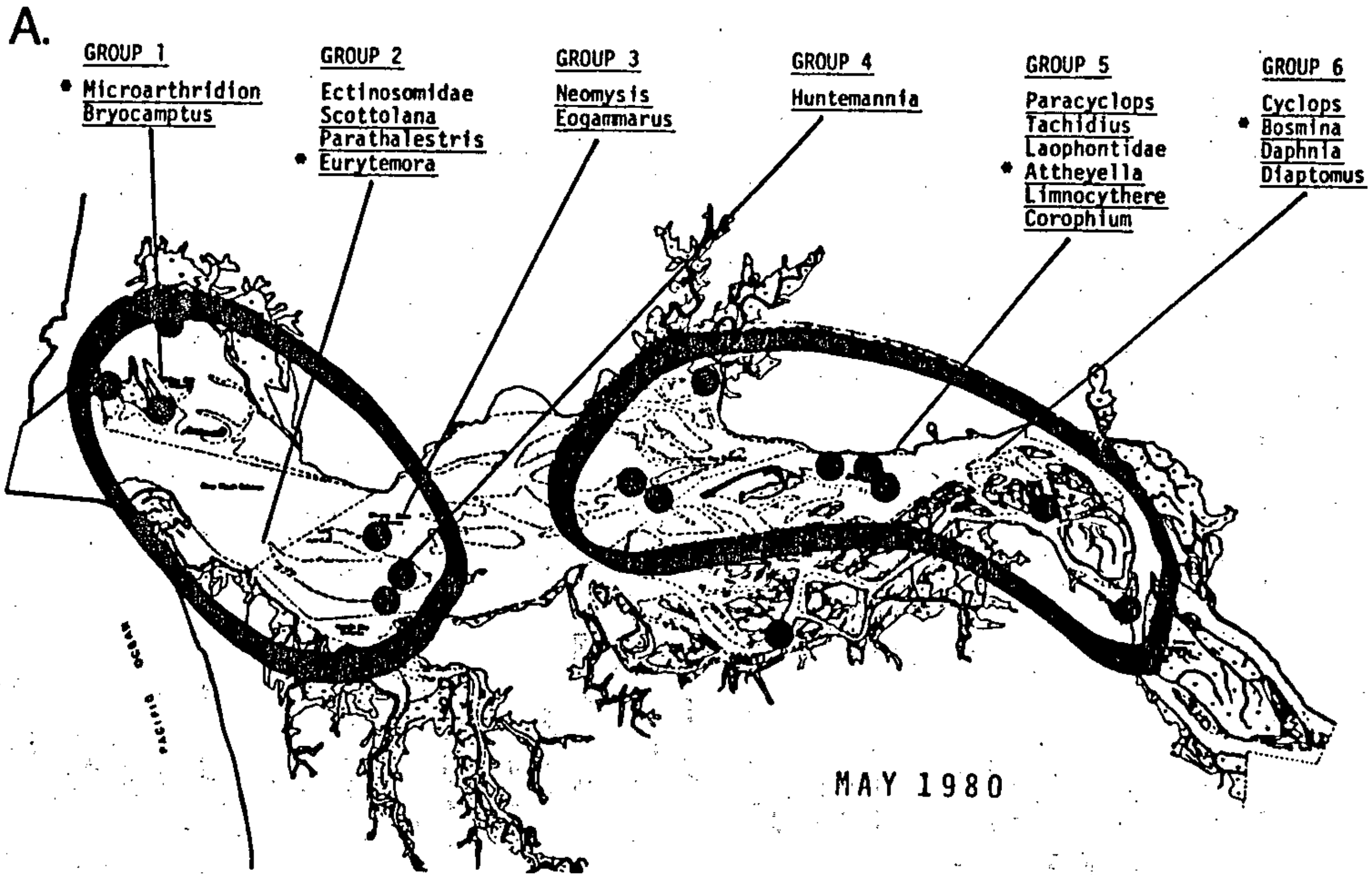


Figure 7.32. Distribution of epibenthic zooplankton assemblage clusters in the Columbia River Estuary during three hydrologic seasons:
(A) high flow season (May 1980);
(B) low flow season (October 1980); and
(C) fluctuating flow (February 1981). (Simenstad 1984)

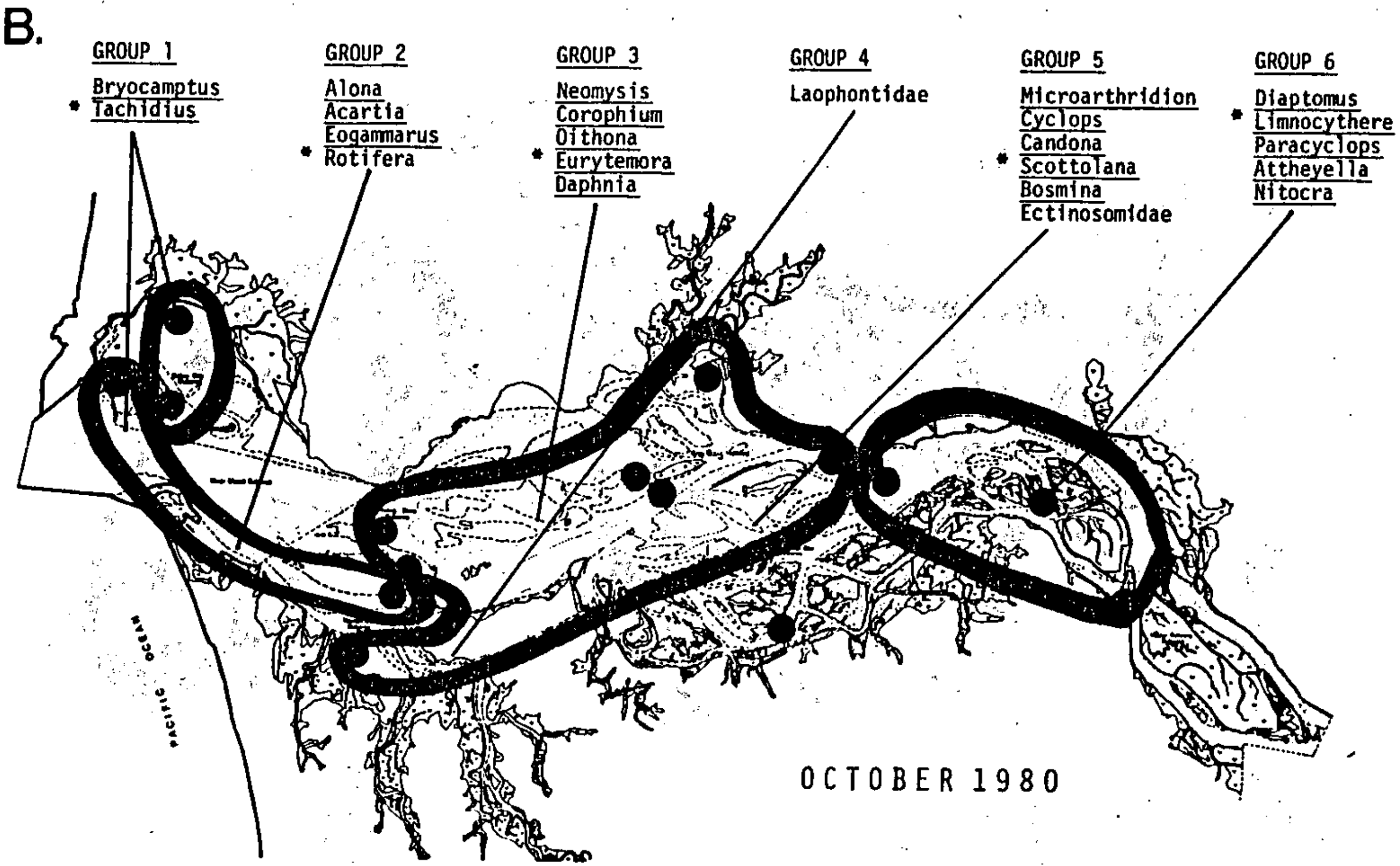


Figure 7.32 (continued).

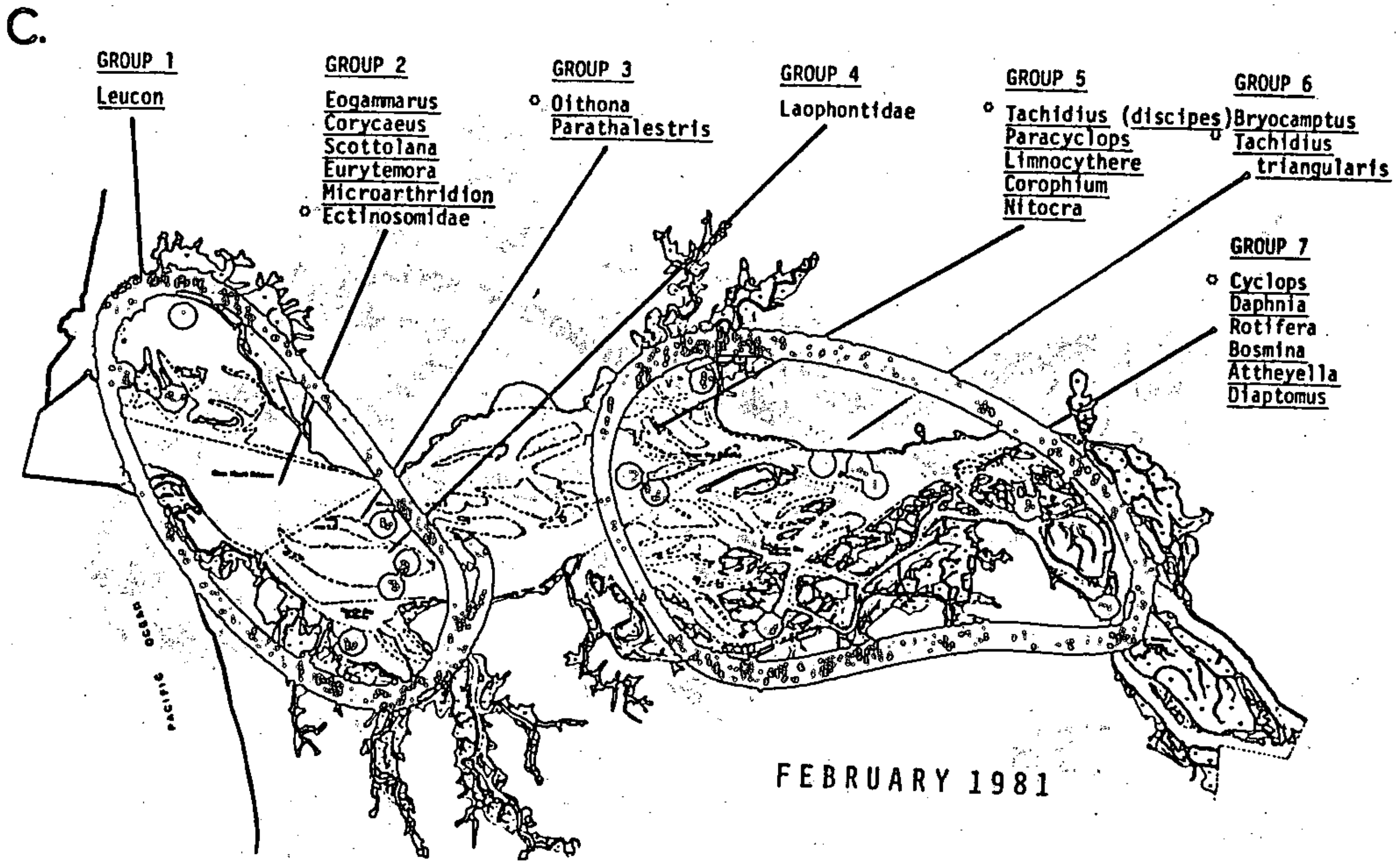


Figure 7.32 (continued).

channels between 30 and 35 km from the entrance; and (5) flats and slopes in the Fluvial Region more than 40 km from the entrance. Taxa clusters were equally complex and included fluvial, euryhaline, and euhaline taxa within several of the six taxa groups delineated. Distribution of taxa groups characterized by depositfeeding euryhaline harpacticoids (including Scottolana, Microarthridion and Ectinosomidae) extended to the upriver boundary of the estuarine mixing zone. The Baker Bay assemblage was still characterized by Bryocamptus.

During the fluctuating flow season, represented by the data from February 1981, the distribution of station and taxa groups (Figure 7.32c) resembled that of the high flow season. Seven taxa clusters again discriminated among estuarine (taxa groups #1-#4) and fluvial (taxa groups #5-#7) assemblages. The characteristic estuarine, deposit-feeding harpacticoids, Scottolana, Microarthridion, and Ectinosomidae, were again concentrated in tidal flat and demersal slope habitats in the downriver half of the estuarine mixing zone. One interesting anomaly was the occurrence of the presumably estuarine harpacticoids Bryocamptus and Nitocra within the tidal-fluvial zone at this time.

It should be remembered that these characterizations of deposit-feeding infauna and epifauna are actually very general categorizations of what are often very flexible feeding modes. For example, the deposit-feeding tentaculate polychaete Pygospio elegans has been observed to suspension feed via both mucous net and palps as well as to feed on surface deposits, and another tentaculate species, P. kempi, is so versatile in feeding modes as to be both suspension feeder and predator as well as a deposit feeder (Hempel 1957 a & b; Taghon et al. 1980; Jumars et al. 1982). Similarly, the tellin bivalve Macoma balthica can capture food particles either by raising the incurrent siphon into the water column and circulating water or by vacuuming the sediment surface around its position, thus variably allocating 10-40% of its life to suspension feeding and 60-90% to deposit feeding (DeWilde 1975). The potential omnivorous feeding capability of the estuarine calanoid copepod, Eurytemora affinis, is yet another example.

Suspension Feeding

Benthic Infauna

Although many deposit-feeding infauna may at times switch to suspension-feeding modes, as described above, only two species of benthic infauna common to the estuary, the bivalves Corbicula manilensis and Mya arenaria, can be classified as true suspension feeders. Reciprocal averaging of numeric data from the distributional survey indicated that Corbicula was a dominant member of the unique group (#1) characterizing the tidal-fluvial zone of the estuary. Mya arenaria were collected only in the plume and ocean zone and at the downriver end of the estuarine mixing zone, principally in Baker Bay.

Epibenthic Zooplankton

As described earlier under the Deposit-Feeding section, two components of the epibenthic zooplankton assemblages in the estuary can be considered suspension feeders, the dominant estuarine calanoid copepod Eurytemora affinis and the diverse freshwater cladocerans and cyclopoid copepods which are imported to the estuary from the river. In this latter fluvial assemblage, the predominant taxa are Bosmina longirostris, Daphnia spp., and Cyclops spp. (Table 7.31). Expansion and contraction of this assemblage with the extent and magnitude of riverine discharge into the estuary is indicated in Figures 7.32a-c. During both periods of high discharge, the fluctuating flow and the high flow seasons, these and other, less-prominent freshwater zooplankters (e.g., Diaptomus, Paracyclops, rotifers) were found in abundance in the epibenthos as far downriver as Tongue Point and usually comprised discrete taxa groups (e.g. #6, Figure 7.32a). Eurytemora, on the other hand, characterized the estuarine assemblages which were confined to the downriver half of the estuarine mixing zone during the high discharge periods.

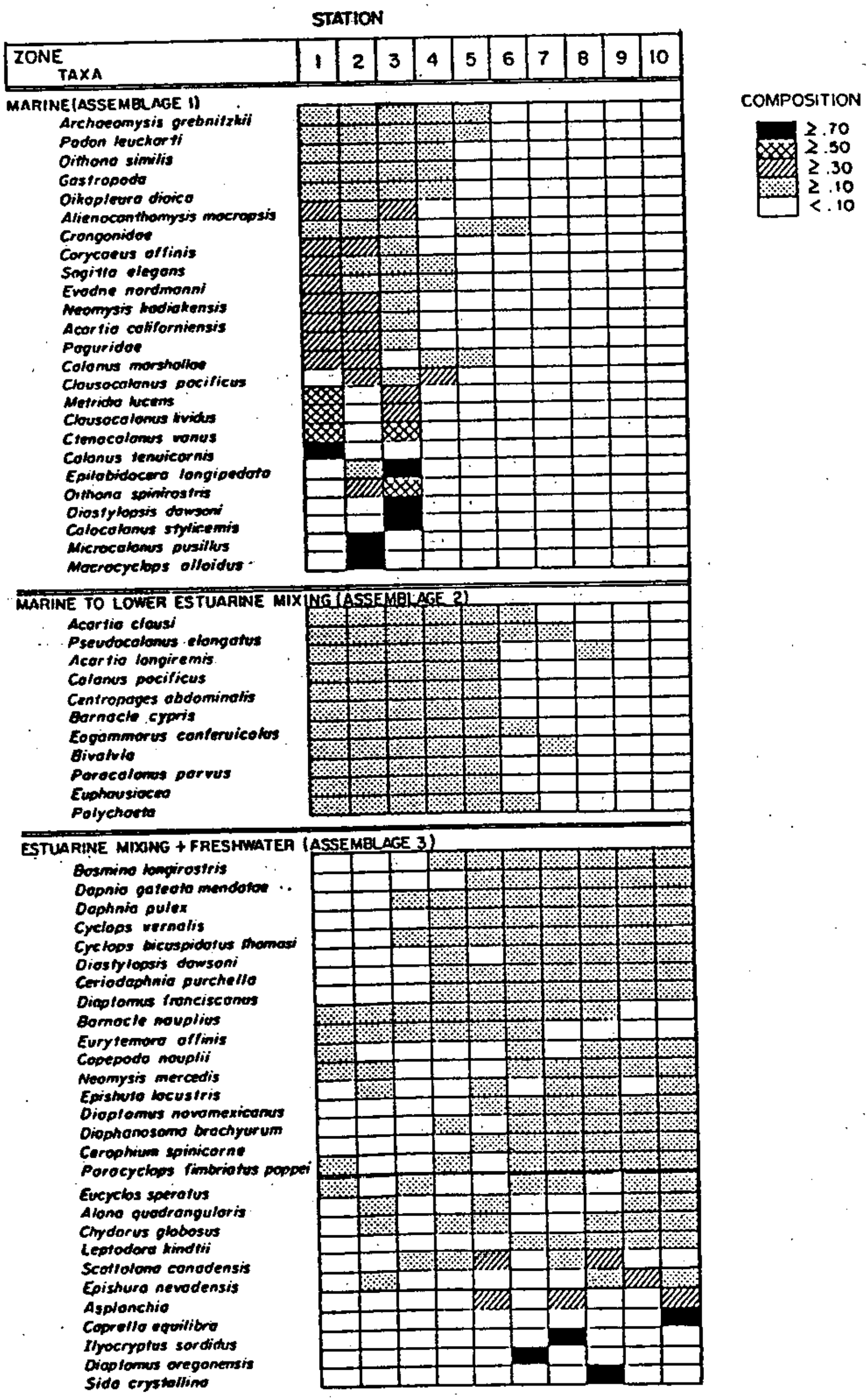
During the low flow season, however, distribution and taxa associations of both groups changed dramatically (Figure 7.32c). Eurytemora affinis became widely distributed throughout the estuarine mixing zone and was found as far up the estuary as Grays Bay-Harrington Point. Perhaps reflecting the effects of the increased and/or deeper mixing of the water column at this time, the composition of almost all the assemblages above the plume and ocean zone became more heterogeneous with the incorporation of the suspension-feeding fluvial taxa into deposit-feeding estuarine harpacticoid assemblages. At the extreme, rotifers were found clustered with sub-plume marine calanoid taxa such as Acartia (group #2, Figure 7.32c). Thus, during this season, the epibenthic zooplankton throughout the estuary might be considered to be relatively equally composed of suspension and deposit feeders, although densities of the two functional feeding groups differ among habitats and regions.

Pelagic Zooplankton

A diverse group of cladocerans and cyclopoid and calanoid copepods composed the pelagic zooplankton assemblages along the main navigation channel of the estuary (Jones and Bottom 1984). Among the prominent (occurring in more than 1000 organisms m^{-2} or frequently at more than three stations) taxa were seven species of cladocerans, ten species of calanoids, five species of cyclopoids, and a larvacean; in addition, undifferentiated early life history stages of bivalves, barnacles, and euphausiids were also common or abundant (Table 7.33). The dominant taxa in terms of both distribution, frequency of occurrence, and abundance in the estuary were Daphnia spp., Bosmina longirostris, Diaptomus ashlandi, Pseudocalanus elongatus, Eurytemora affinis, Acartia clausi, and Cyclops spp., the first three of which are freshwater taxa which originate from the Columbia River above the estuary.

Numerical classification (hierarchical cluster analysis) of the (10 stations x 13 dates) pelagic zooplankton density data reinforced the importance of seasonal variation in estuarine mixing and salinity intrusion which was illustrated by similar analyses of the epibenthic zooplankton and fish data. Clustering of the data from collections during the high flow season indicated four station groups and three

Table 7.33. Distribution of zooplankton in the Columbia River Estuary expressed as pe cent of the average abundance ($\log_{10} x + 1$) during the year (Jones and Bottom 1984).



STATION

ZONE TAXA	1	2	3	4	5	6	7	8	9	10
MARINE (ASSEMBLAGE 1)										
Archaeomysis grebnitzkii	░	░	░	░	░					
Podon leuckarti	░	░	░	░	░					
Oithona similis	░	░	░	░						
Gastropoda	░	░	░	░						
Oikopleura dioica	░	░	░	░						
Alienocanthomysis macropsis	▨	░	▨							
Crangonidae	░	░	░		░	░				
Corycaeus affinis	▨	▨	░							
Sagitta elegans	▨	░	░	░						
Evadne nordmanni	▨	░	░	░						
Neomysis kadiakensis	▨	▨	░							
Acartia californiensis	▨	▨	░							
Paguridae	▨	▨	░							
Calanus marshallae	▨	▨		░	░					
Clausocalanus pacificus		▨	░	▨						
Metridia lucens	▩		▨							
Clausocalanus lividus	▩		▨							
Ctenocalanus vanus	▩		▩							
Calanus tenuicornis	■									
Epilabidocera longipedata		░	■							
Oithona spinirostris		▨	▩							
Diastylopsis dawsoni			■							
Calocalanus styliremis			■							
Microcalanus pusillus		■								
Macrocyclops alloidus		■								
MARINE TO LOWER ESTUARINE MIXING (ASSEMBLAGE 2)										
Acartia clausi	░	░	░	░	░	░				
Pseudocalanus elongatus	░	░	░	░	░	░	░			
Acartia longiremis	░	░	░	░	░			░		
Calanus pacificus	░	░	░	░	░					
Centropages abdominalis	░	░	░	░	░					
Barnacle cypris	░	░	░	░	░					
Eogammarus confervicolus	░	░	░	░	░	░				
Bivalvia	░	░	░	░	░		░			
Paracalanus parvus	░	░	░	░	░					
Euphausiacea	░	░	░	░	░					
Polychaeta	░	░	░	░	░	░				
ESTUARINE MIXING + FRESHWATER (ASSEMBLAGE 3)										
Bosmina longirostris				░	░	░	░	░	░	░
Dapnia gateata mendotae					░	░	░	░	░	░
Daphnia pulex			░	░	░	░	░	░	░	░
Cyclops vernalis				░	░	░	░	░	░	░
Cyclops bicuspidatus thomasi			░	░	░	░	░	░	░	░
Diastylopsis dawsoni				░		░	░	░	░	░
Ceriodaphnia purchella				░	░	░	░	░	░	░
Diaptomus franciscanus				░	░	░	░	░	░	░
Barnacle nauplius	░	░	░	░	░	░	░	░		
Eurytemora affinis	░	░	░	░	░	░				
Copepoda nauplii	░					░		░	░	░
Neomysis mercedis	░	░				░	░	░	░	░
Epishuta lacustris		░			░		░	░		░
Diaptomus novamexicanus					░	░	░	░	░	░
Diaphanosoma brachyurum				░		░	░	░	░	░
Cerophium spinicorne					░	░	░	░	░	░
Paracyclops fimbriatus poppei	░			░		░	░	░	░	░
Eucyclos speratus	░		░			░	░		░	░
Alona quadrangularis		░			░				░	░
Chydorus globosus		░		░	░			░	░	░
Leptodora kindtii						░	░	░	░	░
Scottolana canadensis			░	░	▨		░	▨		
Epishura nevadensis		░						░	▨	░
Asplanchia					▨		▨			▨
Caprella equilibra										■
Ilyocryptus sordidus							■			
Diaptomus oregonensis						■				
Sida crystallina								■		

COMPOSITION

■ ≥ .70
▩ ≥ .50
▨ ≥ .30
░ ≥ .10
□ < .10

taxa assemblages. A plume-and-ocean/lower-estuarine-mixing zone assemblage characterized by stenohaline marine taxa (*Archaeomysis grebnitzkii*, *Acartia clausi*, *Centropages abdominalis*, *Paracalanus parvus*, *Pseudocalanus elongatus*) was located primarily within 15 km to 20 km of the mouth of the estuary (Figure 7.33a). A truly estuarine assemblage dominated by *Eurytemora affinis* was relatively isolated in the central estuarine mixing zone. A tidal-fluvial assemblage composed of freshwater taxa (*Bosmina longirostris*, *Cyclops bicuspidatus thomasi*, *Daphnia ashlandi*) encompassed two upriver station groups, extending into the middle of the estuarine mixing zone under the high flow conditions. The boundary in the distributions of the marine and freshwater taxa appeared to form a secondary division of the estuarine mixing zone.

During the low flow season, three station groups and two taxa assemblages were delineated (Figure 7.33b). Plume and ocean zone taxa (including *Acartia longiremis*) extended more than 30 km upriver, across two station groups. The low flow conditions and increased salinity intrusion also caused the estuarine *Eurytemora* assemblage to overlap with the freshwater (including *Daphnia galeata mendotae*) assemblage over the two upriver station groups.

Conditions during the fluctuating flow season produced station-taxa clusters similar to those resulting from the high flow season data (Figure 7.33c). However, due to the greater downriver extension of the freshwater assemblage, there was not a distinct secondary division of the estuarine mixing zone even though the estuarine mixing zone assemblage (including the epibenthic harpacticoid *Scottolana canadensis*) occupied approximately the same position in the estuary.

These seasonal structures of pelagic zooplankton support and elucidate the conclusions of Haertel and Osterberg (1967) that three major groups - one freshwater, one "slightly brackish" water, and one "salt intrusion" - occupy the estuary; other than due to taxonomic revisions, there were no basic differences in the taxa composing Haertel and Osterberg's groups and those defined by Bottom et al. (1984).

Predation

Benthic Infauna

Benthic infauna assemblages contain few predators, such as the errantate polychaetes *Eteone* spp. and *Nephtys californiensis* and the amphipod *Eogammarus confervicolus*. *Eteone* spp. and *Nephtys californiensis* were relatively common in most habitats of the plume and ocean zone, particularly so in more coarse-grained channel and unprotected littoral flat habitats. *Eogammarus confervicolus* occurred in nearly all habitats of the plume and ocean and estuarine mixing zones and extended into many tidal-fluvial zone habitats.

Motile Macroinvertebrates

The two large, epibenthic crustaceans, the sand shrimp, *Crangon franciscorum*, and Dungeness crab, *Cancer magister*, are also prominent predators (Simenstad 1984). *Cancer magister* was almost completely

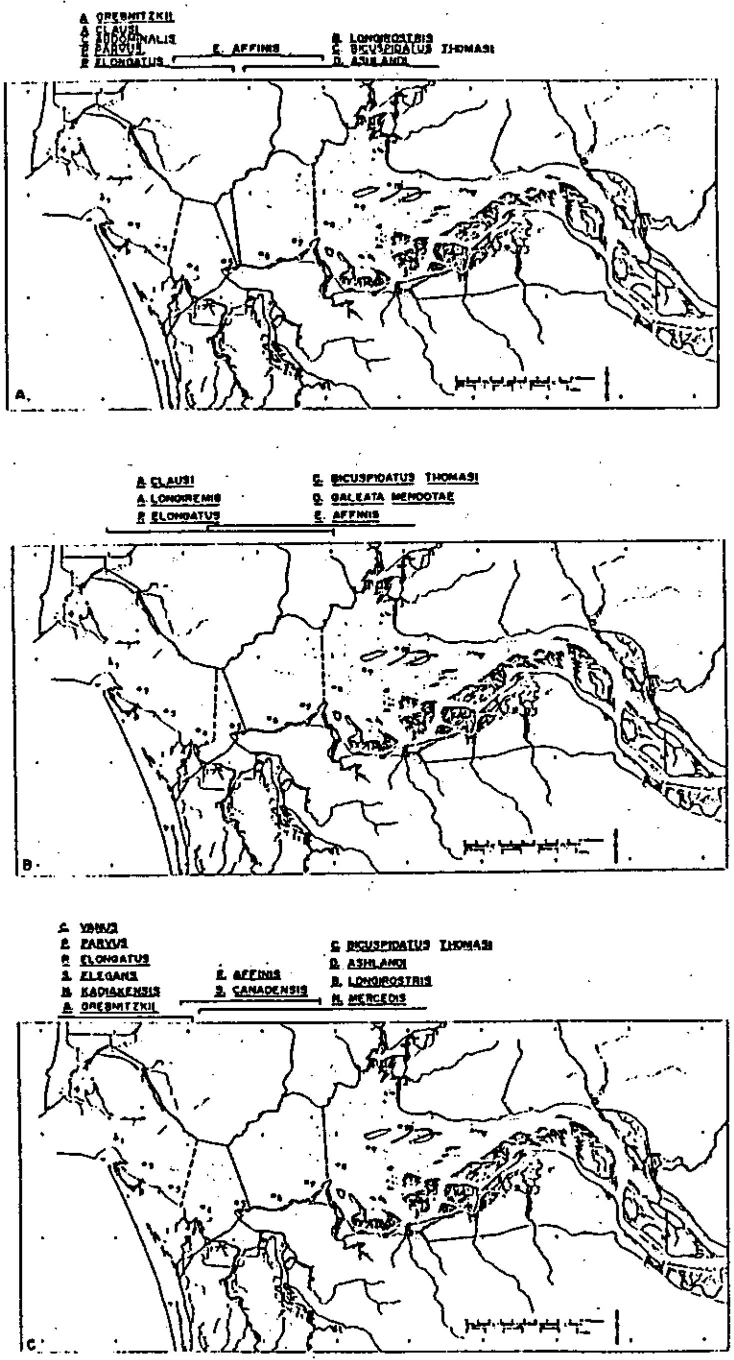


Figure 7.33. Distribution of pelagic zooplankton taxa in the Columbia River Estuary for high flow (A), low flow (B), and fluctuating flow (C) hydrologic seasons (Jones and Bottom 1984).

restricted to channel bottom habitats in the plume and ocean zone but was found on tidal flat habitats (i.e., Baker Bay) during the low flow period (Figure 7.34). Thus, Crangon franciscorum is the predominant macroinvertebrate predator in the estuary. During both the fluctuating flow and the high flow seasons, sand shrimp populations are concentrated within 20 km of the estuary's mouth, and particularly in the tidal flat habitat at Youngs Bay. Coincident with increased salinity intrusion up the estuary during the low flow season, however, sand shrimp distribution expands to Grays Bay, approximately 32 km from the estuary's entrance.

Although the distribution of Dungeness crab reported in these studies coincides with that described by Haertel and Osterberg (1967), other sampling efforts in the estuary (Durkin et al. 1981) suggest that Dungeness crab distribution and abundance may be extremely variable on tidal, diel, seasonal, and annual scales. In contrast to the CREDDP macroinvertebrate data, Durkin et al. (1981) found crab in the navigation channel, although in relatively low abundance, as far as 25 km upriver of the mouth of the estuary (near Astoria) during the fluctuating flow season; however, comparatively high abundances of crabs were reported in the channel bottom habitat 15 km from the mouth of the estuary (i.e., Tansy Point) during both fluctuating flow and high flow months.

Haertel and Osterberg's (1967) documentation of sand shrimp occurrence in all salinity regimes (i.e., limnetic [0-0.5 o/oo] to euhaline [about 30 o/oo]) differs from evidence presented here that the distribution of C. franciscorum is confined within euhaline to oligohaline waters.

Epibenthic and Pelagic Zooplankton

Among the zooplankters found within the epibenthic region and the water column, the mysids Neomysis mercedis and Archaeomysis grebnitzkii can be considered predators even though they also have the capability to feed effectively on diatoms and detritus (see Consumption section). The estuarine-oligohaline species, Neomysis mercedis, was the more widely distributed of the two species, and appeared to be constrained more by the increased intrusion of saline plume and ocean zone waters during the low flow season than by the low salinity influences of high river discharge during the high flow season (Figure 7.35). In contrast, the less-abundant, euryhaline-marine Archaeomysis grebnitzkii was restricted to downriver of Astoria under high flow conditions and expanded into the upper half of the estuarine mixing zone (i.e., Miller Sands) only under low flow conditions (Figure 7.33a).

Larval Fishes

All larval fishes in the estuary are secondary consumers. Among the eleven taxa documented by Jones and Bottom (1984), only prickly sculpin (Cottus asper) and undifferentiated smelt (Osmeridae) larvae were ever found in abundance in the estuary.

Prickly sculpin larvae occurred throughout the estuary between

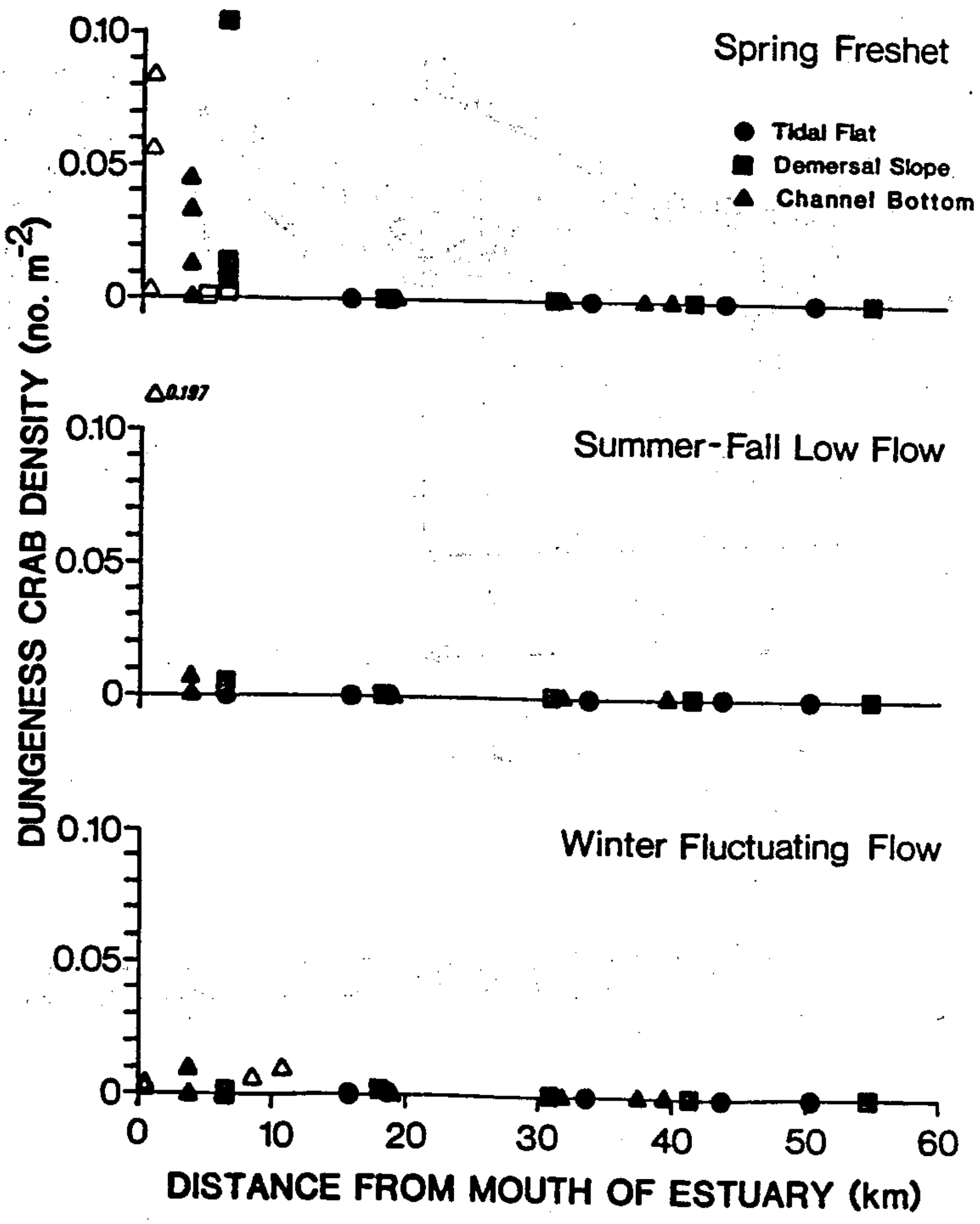


Figure 7.34. Spatial distribution (km from mouth of estuary) of Dungeness crab (Cancer magister) density (individuals m^{-2}) during three hydrologic seasons and among three habitats in the Columbia River Estuary, March 1980 - July 1981. Open symbols indicate crab densities from comparable CREDDP collections by NMFS (Simenstad 1984).

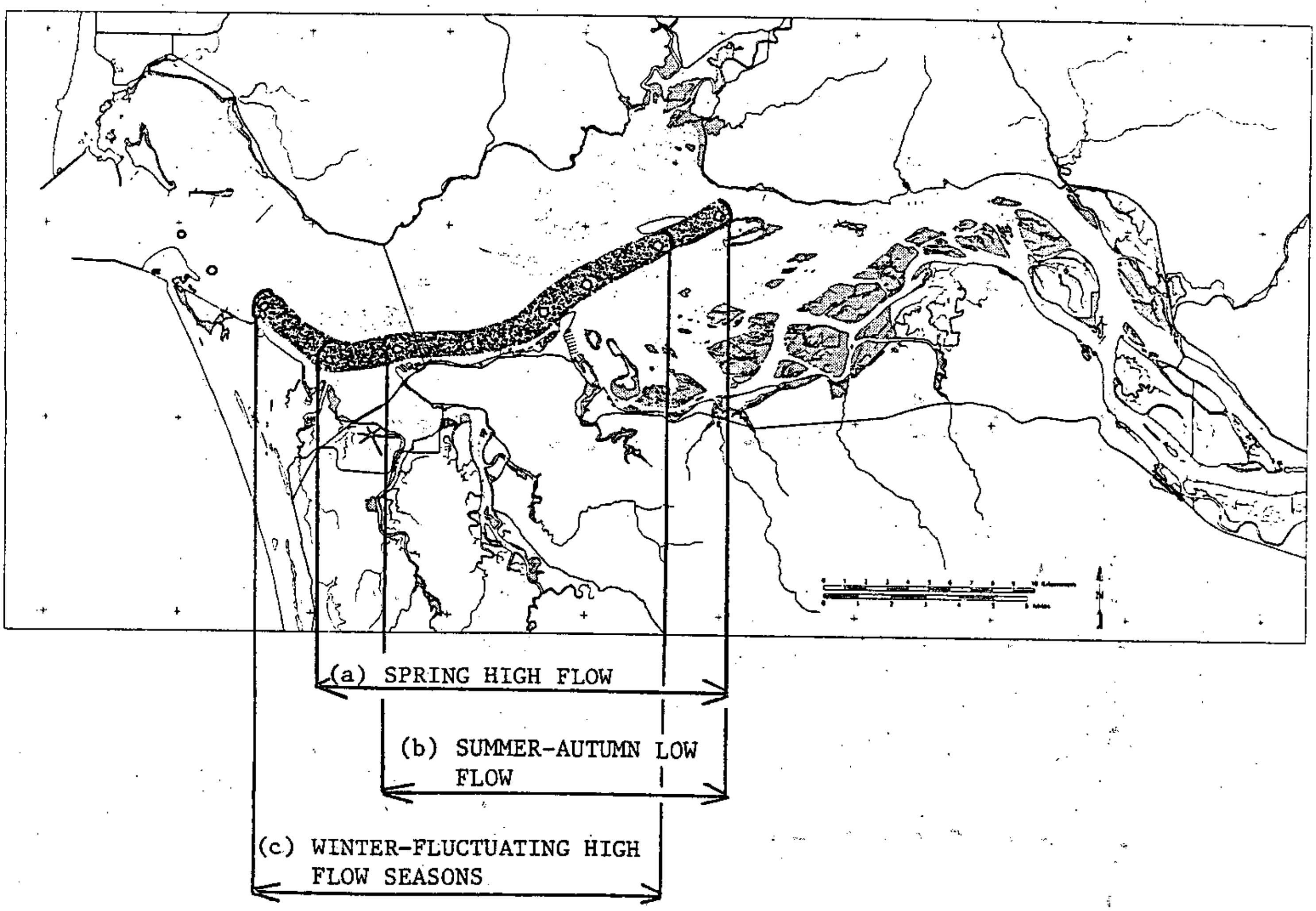


Figure 7.35. Distribution of *Neomysis mercedis* in the Columbia River Estuary during (a) high flow, (b) low flow, and (c) fluctuating flow seasons.

April and August but maximum abundance was documented in the region between Youngs Bay and Tongue Point, i.e., within the spatial range of the turbidity maximum zone, from late April through late May. Osmerid larvae, which were more abundant than prickly sculpin, were distributed throughout the estuary between January and late May but were concentrated above Trestle Bay during late April.

Jones and Bottom (1984) applied cluster analysis to the larval fish data separate from that of the pelagic zooplankton. They described three to four taxa assemblages which changed dramatically in distribution and composition during the three hydrologic seasons due to phases in recruitment and metamorphosis as well as seasonal circulation changes (Figure 7.36). The high flow season marked the most extensive influx of fish larvae (and eggs, which are not consumers) from the plume and ocean waters into the estuary (Figure 7.36a). Four taxa assemblages were identified, including two of predominantly marine fish eggs (*Citharichthys* spp., *Engraulis mordax*, Pleuronectidae) and larvae (*Ammodytes hexapterus*, Gobiidae, *Engraulis mordax*, *Leptocottus armatus*, *Clupea harengus pallasi*) which extend 30 to 35 km upriver from the mouth of the estuary, one of *Thaleichthys pacificus* larvae which is restricted to the lower 15 km of the estuary, and one of *Cottus asper* larvae and osmerid eggs and larvae which is distributed throughout the estuary.

During the low flow season (Figure 7.36b), the general fish eggs assemblage was actually reduced in distribution to the lower 20 km to 25 of the estuary. An assemblage characterized by Pacific herring larvae (*C. h. pallasi*) occupied the estuarine mixing zone. *C. asper* designated another assemblage that occupied the upriver portion of the plume and ocean zone and all of the estuarine mixing zone.

Taxa assemblages were less diverse and station groups clustered downriver during the fluctuating flow season (Figure 7.36c). Pleuronectid eggs were present only in the plume and ocean zone, *Parophrys vetulus* larvae extended from that zone into the lower half of the estuarine mixing zone, and osmerid larvae were again (as in the high flow season) spread throughout the estuary. However, the number of collections during this season was limited and may underrepresent the diversity of the fish eggs and larvae, which are known to begin appearing in late winter in the estuary (Misitano 1977).

Juvenile and Adult Fishes

All juvenile and adult fishes fall within the Predator state variable. Although 75 species of fish were collected during the 18-month synoptic fish survey, several of which occurred in a number of different life history stages (Table 7.34), only 42 (56%) were represented by ten or more individuals (McConnell et al. 1983). Of these, ten (asterisks, Table 7.34) were treated as key species due to their economic or ecological importance: American shad (*Alosa sapidissima*), Pacific herring (*Clupea harengus pallasi*), northern anchovy (*Engraulis mordax*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), longfin smelt (*Spirinchus thaleichthys*), shiner perch (*Cymatogaster aggregata*), Pacific staghorn sculpin (*Leptocottus armatus*), English sole (*Parophrys vetulus*), and starry

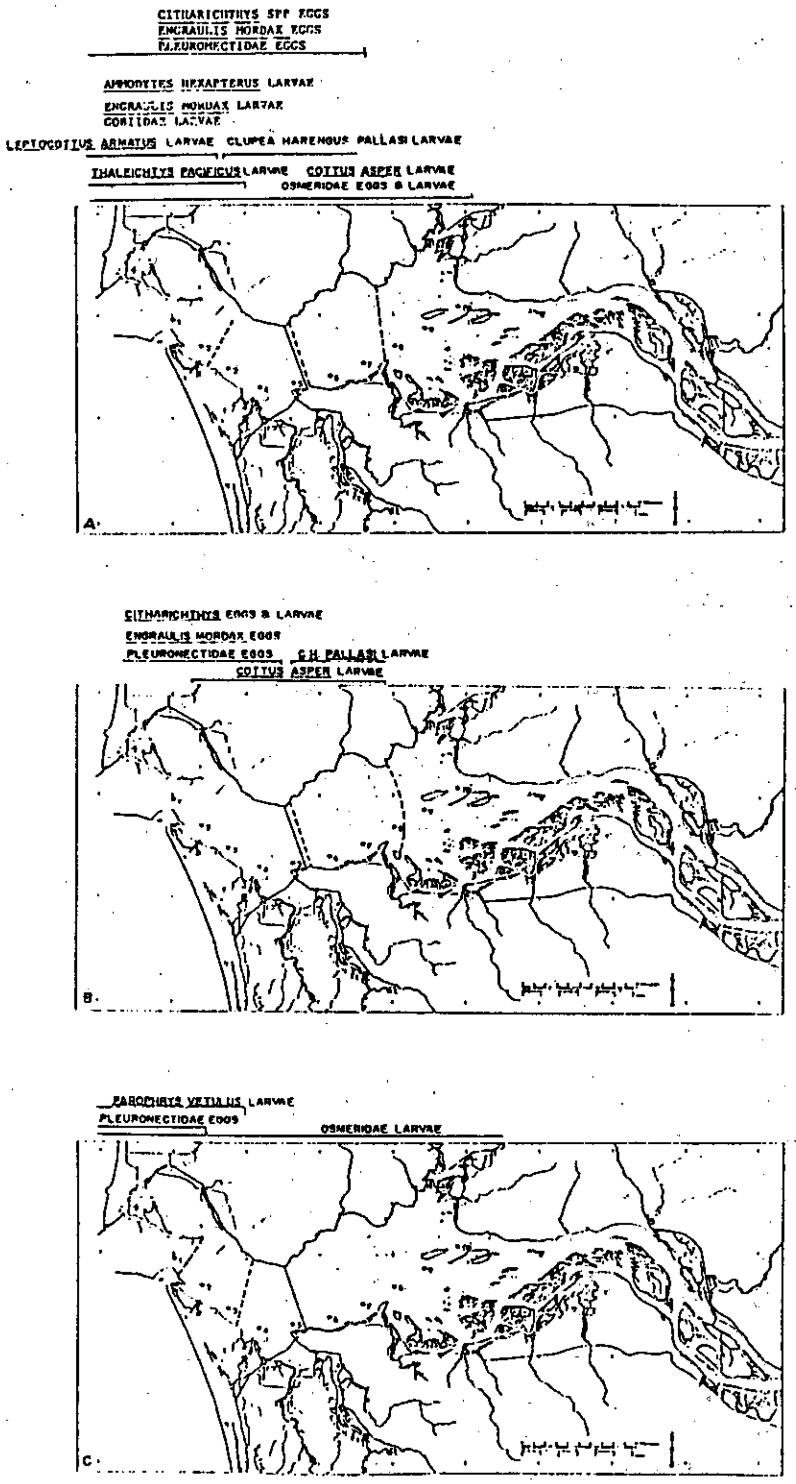


Figure 7.36. Distribution of fish eggs and larvae in the Columbia River Estuary for high flow (A), low flow (B), and fluctuating flow (C) hydrologic seasons (Jones and Bottom 1984).

Table 7.34. Total number and weight of fishes taken during CREDDP sampling in the Columbia River Estuary between February 1980 and July 1981. Asterisks designate CREDDP key species.

COMMON NAME	SCIENTIFIC NAME	Distribution Samples Number	 Weight
Pacific lamprey	*Lampetra tridentata*	40	4,712
River lamprey	*Lampetra ayresi*	47	832
Spiny dogfish	*Squalus acanthias*	37	69,354
Big skate	*Raja binoculata*	12	59,024
Green sturgeon	*Acipenser medirostris*	1	7,600
White sturgeon	*Acipenser transmontanus*	74	78,371
*American shad	*Alosa sapidissima*	9,751	327,001
*Pacific herring	*Clupea harengus pallasi*	19,640	275,333
*Northern anchovy	*Engraulis mordax*	11,238	191,758
Chum salmon	*Oncorhynchus keta*	31	55
*Coho salmon	*Oncorhynchus kisutch*	3,110	82,782
Sockeye salmon	*Oncorhynchus nerka*	74	1,065
*Chinook salmon	*Oncorhynchus tshawytscha*	13,090	135,889
Mountain whitefish	*Prosopium williamsoni*	1	18
Cutthroat trout	*Salmo clarki*	64	11,983
Steelhead	*Salmo gairdneri*	929	84,297
Whitebait smelt	*Allosmerus elongatus*	3,126	33,275
Surf smelt	*Hypomesus pretiosus*	6,831	44,810
Night smelt	*Spirinchus starksi*	1	19
*Longfin smelt	*Spirinchus thaleichthys*	20,957	132,090
Eulachon	*Thaleichthys pacificus*	1,984	60,471
Common carp	*Cyprinus carpio*	61	97,264
Peamouth	*Mylocheilus caurinus*	4,718	315,885
Northern squawfish	*Ptychocheilus oregonensis*	34	4,504
Largescale sucker	*Catostomus macrocheilus*	496	372,777
Yellow bullhead	*Ictalurus natalis*	1	413
Brown bullhead	*Ictalurus nebulosus*	16	2,544
Pacific hake	*Merluccius productus*	7	7,500
Pacific tomcod	*Microgadus proximus*	8m765	239,671
Walleye pollock	*Theragra chalcogramma*	5	6
Threespine stickleback	*Gasterosteus aculeatus*	6,500	9,522
Bay pipefish	*Syngnathus leptorhynchus*	5	6

Table 7.34. (Continued)

Pumpkinseed	Lepomis gibbosus	1	43
Warmouth	Leopmis gulosos	3	33
Bluegill	Lepomis macrochirus	8	722
Largemouth bass	Micropterus salmoides	2	52
White crappie	Pomoxis annularis	53	5,825
Black crappie	Pomoxis nigromaculatus	135	12,488
Yellow perch	Perca flavescens	113	24,235
Redtail surfperch	Amphistichus rhodoterus	41	12,204
*Shiner perch	Cymatogaster aggregata	24,603	277,843
Striped seaperch	Embiotoca lateralis	1	4
Spotfin surfperch	Hyperprosopon anale	41	1,740
Walleye surfperch	Hyperprosopon argenteum	2	59
Silver surfperch	Hyperprosopon cilipticum	8	182
White seaperch	Phanerodon furcatus	1	87
Pile perch	Rhacochilus vacca	5	179
Pacific sandfish	Trichodon trichodon	3	353
Snake prickleback	Lumpenus sagitta	2,189	52,321
Saddleback gunnel	Pholis ornata	43	178
Pacific sandlance	Ammodytes hexapterus	2,399	8,998
Bay goby	Lepidogobius lepidus	1	4
Black rockfish	Sebastes melanops	4	549
Kelp greenling	Hexagrammos decagrammus	8	445
Lingcod	Ophiodon elongatus	11	528
Padded sculpin	Artedius fenestralis	4	89
Coastrange sculpin	Cottus aleuticus	3	21
Prickly sculpin	Cottus asper	4,607	123,117
Buffalo sculpin	Enophrys bison	5	613
Red Irish lord	Hemilepidotus hemilepidotus	1	1
*Pacific staghorn sculpin	Leptocottus armatus	8,622	294,056
Cabezon	Scorpaenichtys marmoratus	2	9
Warty poacher	Ocella verrucosa	3	5
Tubenose poacher	Pallasina barbata	1	2
Pricklebreast poacher	Stellerina xyosterna	38	265
Slipskin snailfish	Liparis fucensis	2	5
Showy snailfish	Liparis pulchellus	32	402

Table 7.34. (Continued)

Kingtail snailfish	*Liparis rutteri*	7	21
Pacific sanddab	*Citharichthys sordidus*	1	320
Speckled sanddab	*Citharichthys stigmaeus*	50	221
Butter sole	*Isopstta isolepis*	295	6,123
*English sole	*Parophrys vetulus*	2,770	29,519
*Starry flounder	*Platichthys stellatus*	19,377	384,539
C-O sole	*Pleuronichthys coenosus*	2	3
Sand sole	*Psettichthys melanostictus*	331	7,154
Larval smelt		280	93
Larval flatfish		794	99
Other larval fish		17	28
Adult coho	*Oncorhynchus kisutch*	8	17,413
Adult chinook	*Oncorhynchus tshawytscha*	9	44,781
Adult steelhead	*Salmo gairdneri*	11	31,973
TOTALS		178,533	3,991,779

flounder (Platichthys stellatus). All of these occurred predominantly as juveniles (subyearlings and young yearlings), less frequently as adults. Other numerically important (more than 1000 captured), but less frequently encountered, species included whitebait smelt (Allosmerus elongatus), eulachon (Thaleichthys pacificus), peamouth (Mylocheilus caurinus), Pacific tomcod (Microgadus proximus), threespine stickleback (Gasterosteus aculeatus), snake prickleback (Lumpenus sagitta), Pacific sand lance (Ammodytes hexapterus), and prickly sculpin (Cottus asper).

Associations of fish taxa and life history stages were defined by hierarchical clustering of the NMFS synoptic survey density data (McConnell et al. 1983) averaged over months representing four seasons: (1) winter, January-March; (2) spring, April-June; (3) summer, July-September; and (4) autumn, October-December. Major clusters were arbitrarily discriminated at the 0.7 level of dissimilarity. More detailed descriptions of these numerical classification methods and their results can be found in Bottom et al. (1984).

Despite considerable differences in fish taxa-life history stage occurrence and densities among the seasonal data, clustering consistently delineated 10 to 12 assemblages (Figure 7.37a-d). Two large groups of demersal fishes were identified from the winter data (Figure 7.41a). One cluster (designated #1 in Figure 7.41) included predominantly marine demersal species--butter sole, sand sole, speckled sanddab, English sole, and shiner perch. The other prominent winter group (#3) was also dominated by estuarine and freshwater demersal taxa, including Pacific tomcod, prickly sculpin, Pacific staghorn sculpin, and starry flounder; an association of pelagic taxa--eulachon, longfin smelt, and American shad--was also included in this group, however. Three clusters (#4, #8, #9) contained juvenile salmon and three others (#2, #6, #10) also contained pelagic schooling forage ("baitfish") fishes (Pacific herring, Pacific sand lance, Northern anchovy, American shad, and longfin smelt). Clusters #7 and #5 included comparatively rare demersal marine and estuarine taxa, respectively.

The increased number of fish taxa-life history stages present in the estuary during the spring expanded the diversity of the cluster dendrogram (Figure 7.37b), although many of the clusters were similar to those delineated from the winter data. Juvenile salmonids, adult American shad, and Pacific herring were associated in the largest cluster (#5).

Marine and estuarine demersal assemblages (#7 and #1, respectively) continued to form the largest, most similar taxa clusters during the summer (Figure 7.37c). Freshwater demersal taxa occurred in assemblage #4. The pelagic assemblage (#2) included Pacific herring, whitebait and surf smelt, northern anchovy, yearling and older American shad, and subyearling chinook salmon. The few juvenile salmonids still remaining in the estuary occurred in assemblage #5.

Composition of the autumn fish taxa assemblages were generally similar to the summer assemblages (Figure 7.37d). The most comparable assemblage (#1; 85% overlap) included starry flounder, Pacific staghorn sculpin, shiner perch, longfin smelt, Pacific tomcod, snake prickleback,

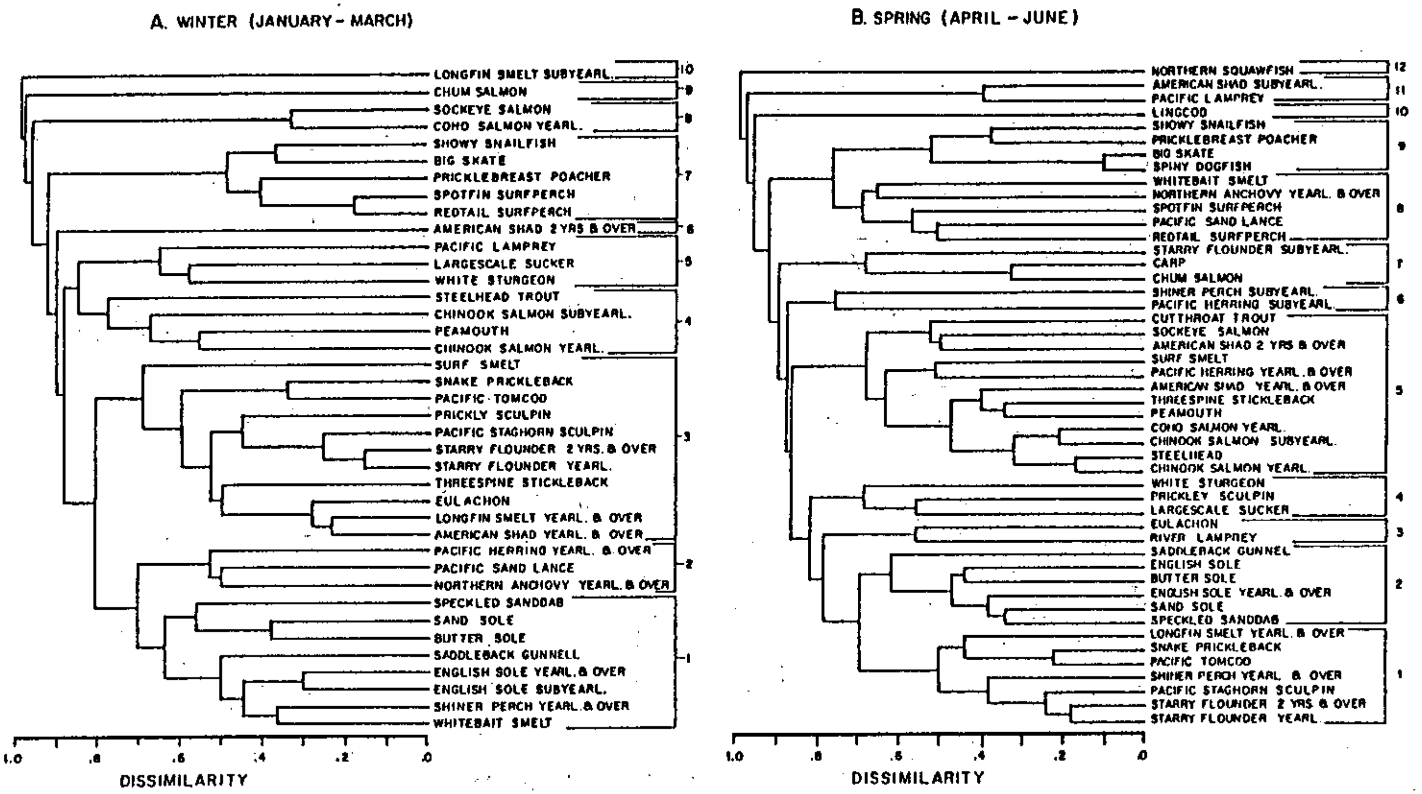
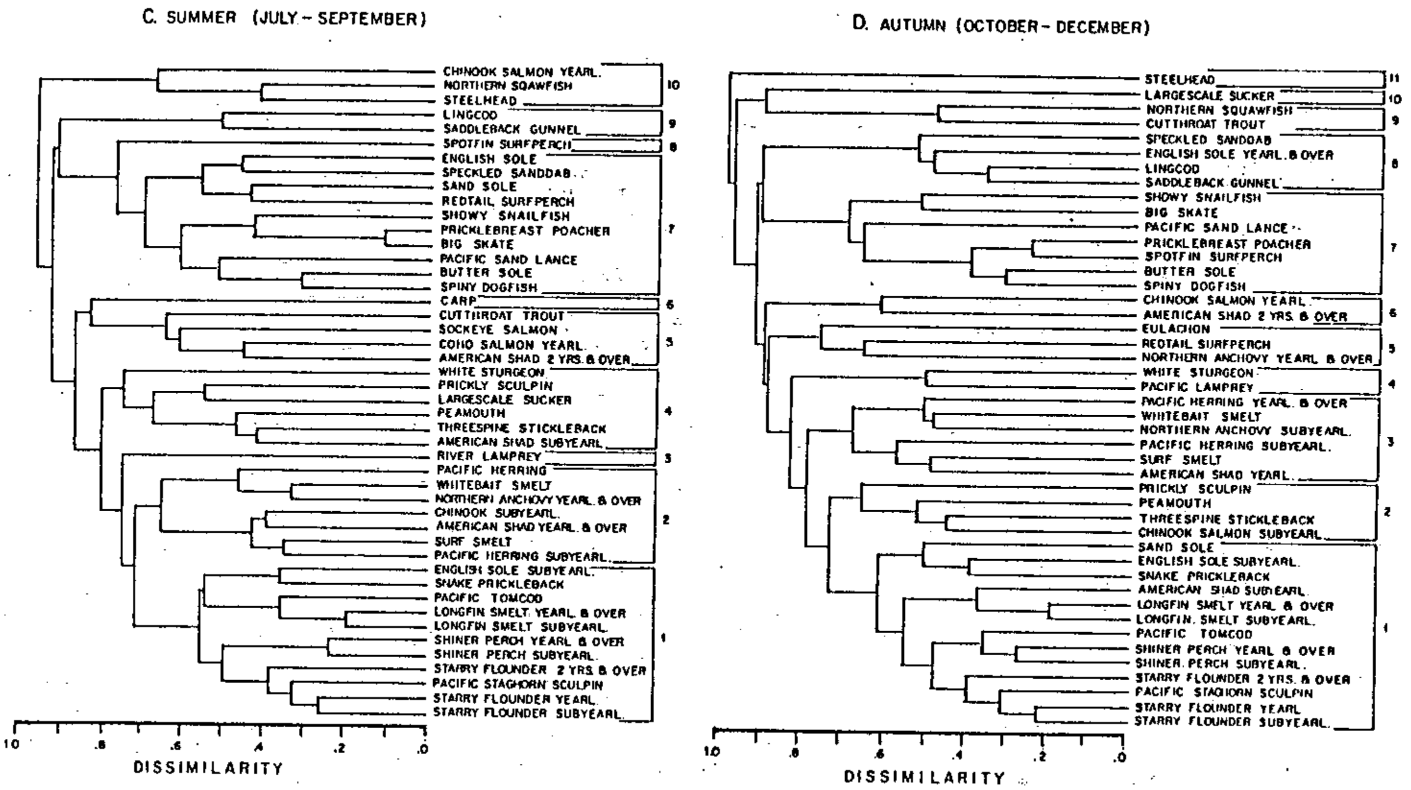


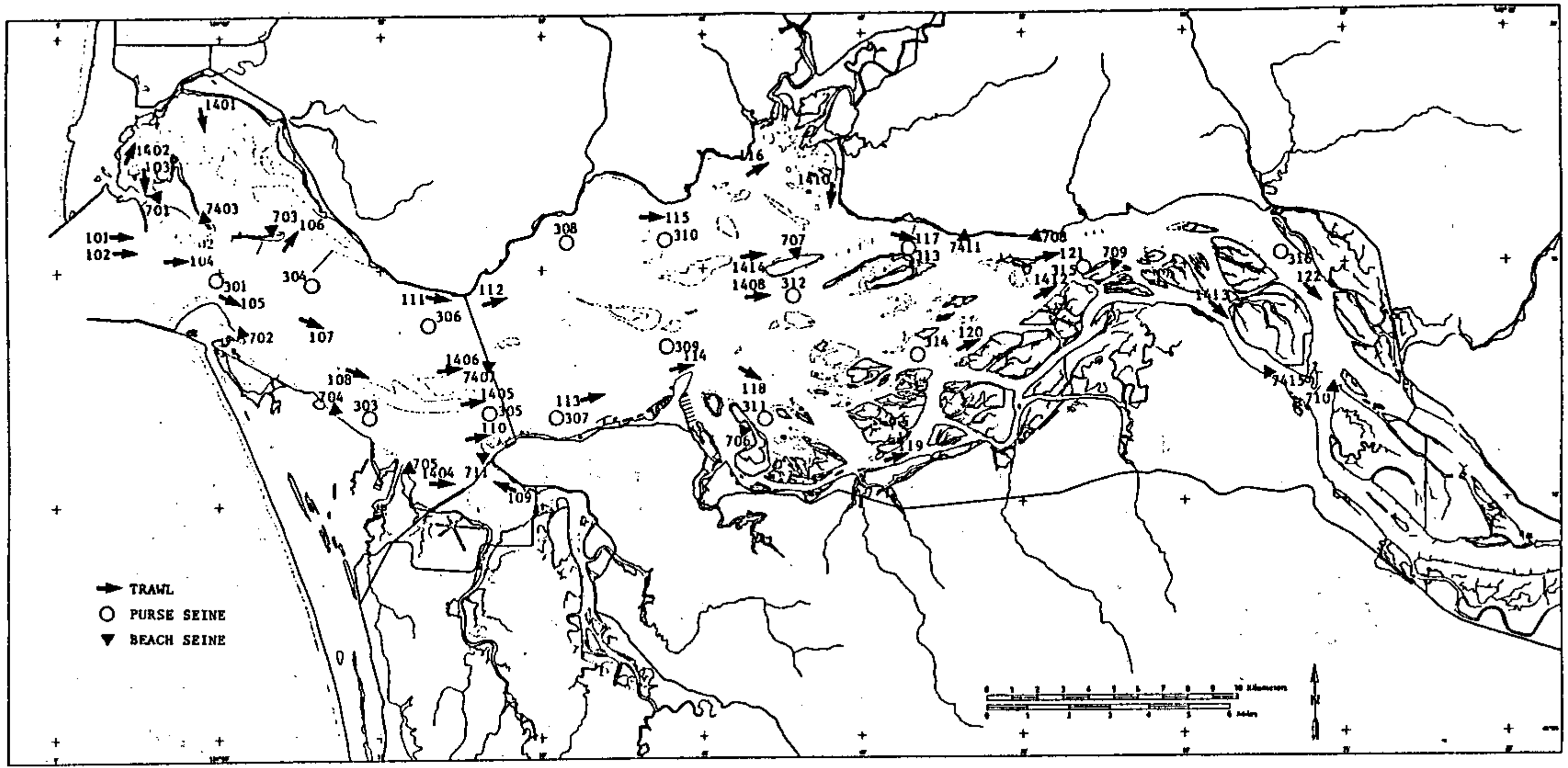
Figure 7.37. Fish taxa-life history assemblages based on seasonally-averaged density data from the Columbia River Estuary. See text for description of seasons.



C. SUMMER (JULY - SEPTEMBER)

D. AUTUMN (OCTOBER - DECEMBER)

Figure 7.37 (continued).



COLUMBIA RIVER ESTUARY: CREDDP FINFISH WORK UNIT STATION LOCATIONS

Figure 7.38. Finfish sampling sites. Four digit station codes with a "4" as the second digit are FRI sampling sites, and all other stations with three digit codes are NMFS sampling stations.

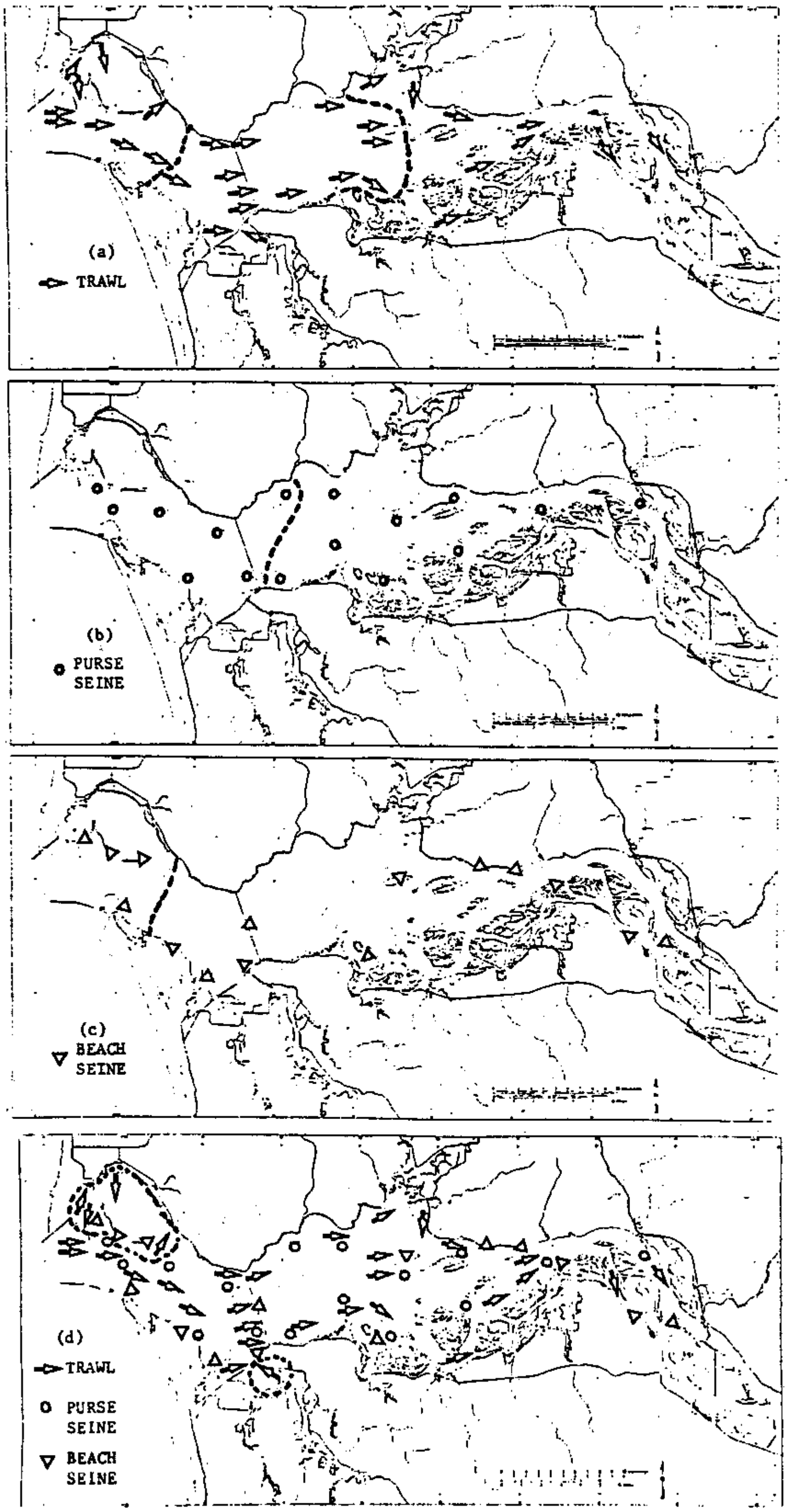


Figure 7.39. Station cluster groups of fish collections by gear (a-c) and combined (d) during high flow period (May 1980) in the Columbia River Estuary.

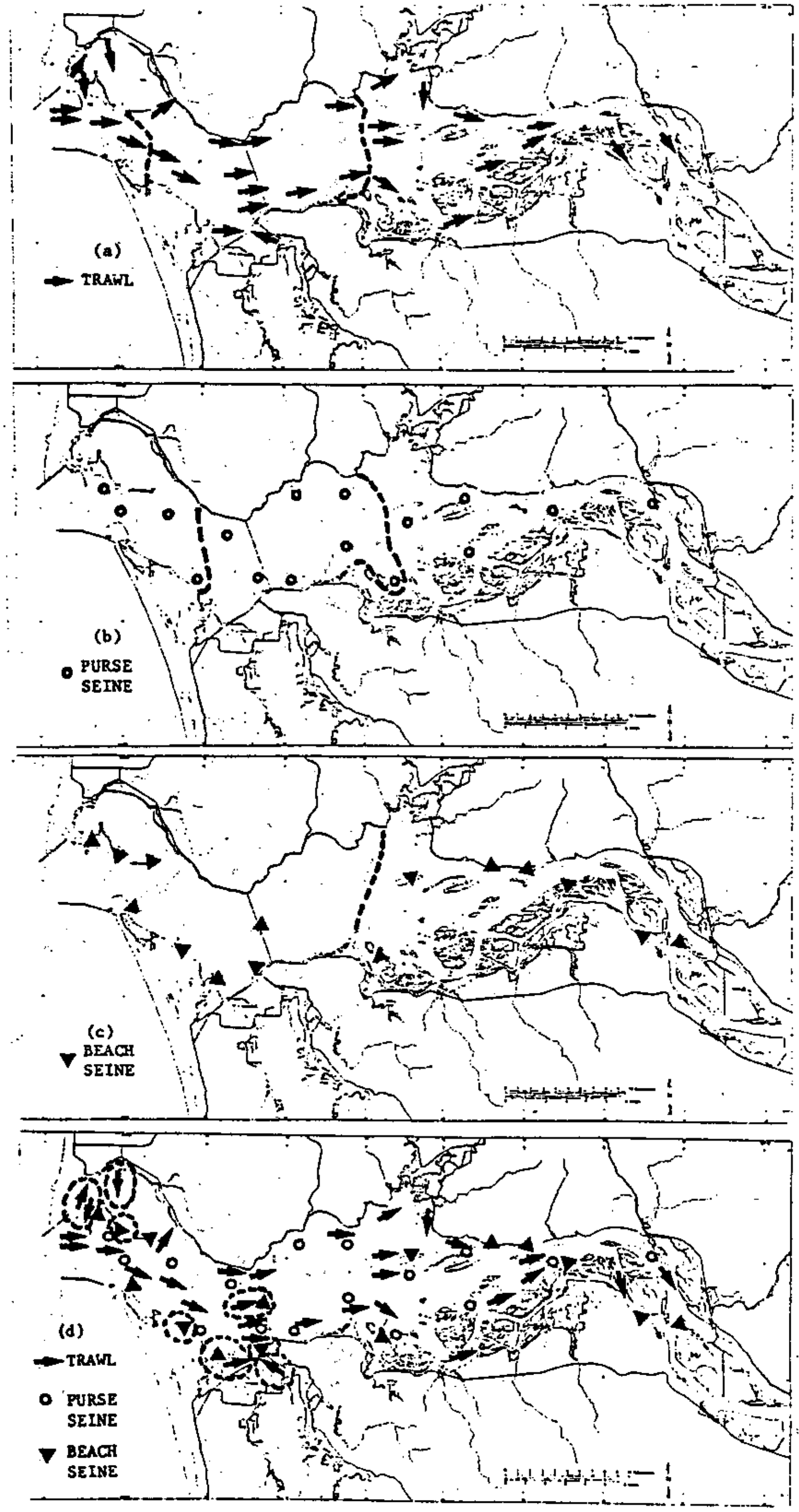


Figure 7.40. Station cluster groups of fish collections by gear (a-c) and combined (d) during low flow (August 1980) in the Columbia River Estuary.

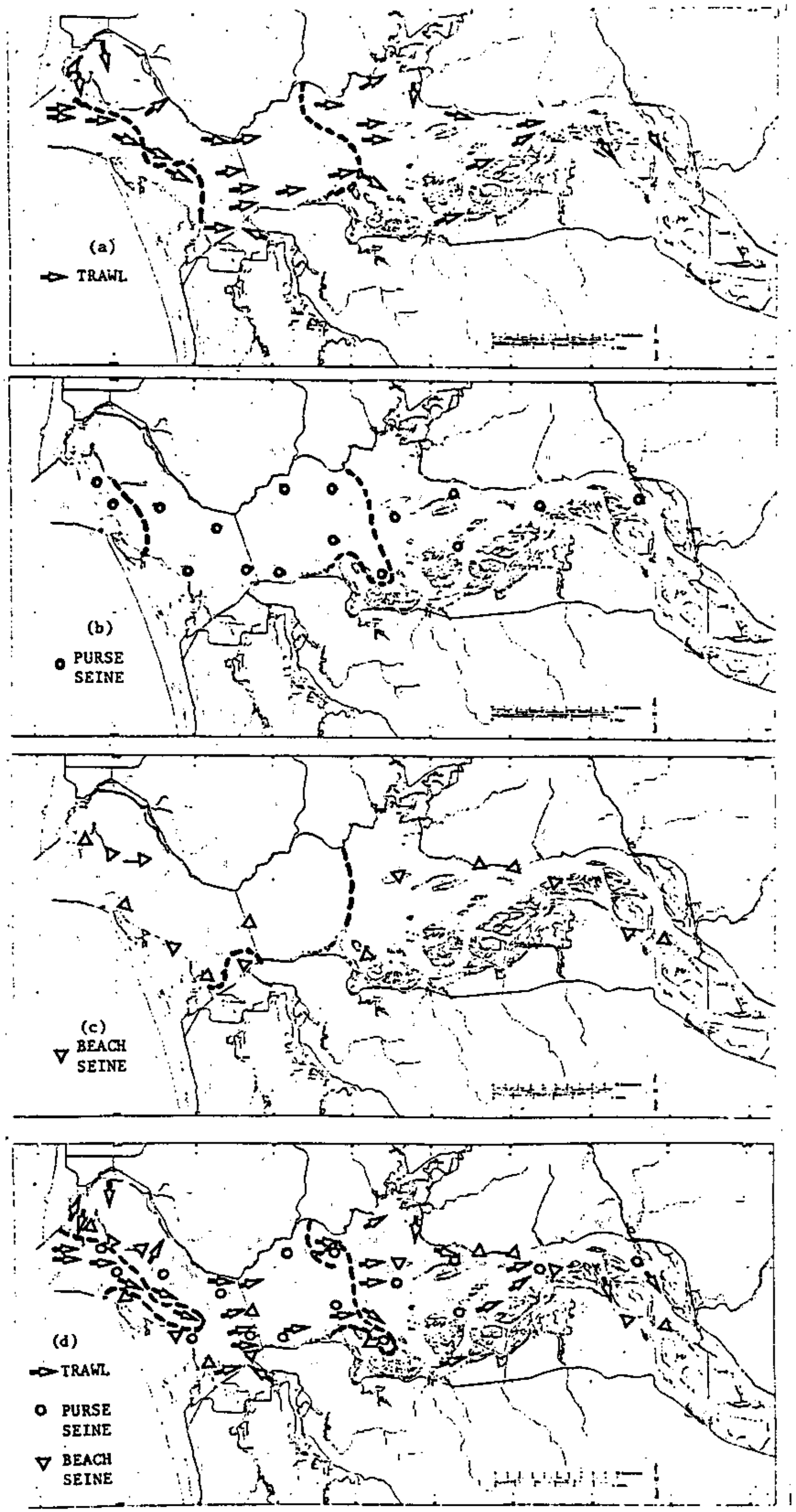


Figure 7.41. Station cluster groups of fish collections by gear (a-c) and combined (d) during fluctuating flow period (January 1981) in the Columbia River Estuary.

and subyearling English sole. The pelagic assemblage (#3), including American shad, surf and whitebait smelt, northern anchovy, and Pacific herring, was also quite similar to the summer pelagic assemblage (#2).

There were several taxa-life history associations which were remarkably persistent throughout all seasons. One of the highest similarity (0.1 to 0.3 dissimilarity) relationships was maintained among early life history stages of Pacific staghorn sculpin and starry flounder. Snake prickleback and Pacific tomcod were also closely associated during the winter and spring .

Spatial distributions of the predominant station groups were determined by hierarchical cluster analysis using species densities as attributes in an average fish density-station data matrix which included data from collections (Figure 7.38) during the NMFS 18-month synoptic survey as well as from the incidental fish catches during coincident Fisheries Research Institute (FRI, University of Washington) sampling of motile macroinvertebrates (Bottom et al. 1984; Simenstad 1984). The FRI collections included habitats not sampled in the NMFS survey, particularly protected embayment tidal flat and demersal slope habitats. After evaluation of the seasonal variation in estuarine circulation (Chapter 3), fish data from three months were selected as representative of the three principal hydrologic seasons in the estuary.

With some modifications, the resulting station clusters generally agreed with the results of seasonally-averaged analyses using just the NMFS synoptic survey data (Bottom et al. 1984). Station clusters during the upriver from season (May 1980) indicated four channel bottom (trawl), two channel water column (purse seine), and three demersal slope (beach seine) groups which indicated an extensive tidal-fluvial zone upriver from Tongue Point, a large estuarine mixing zone extending close to the entrance, and a very small plume and ocean zone (Figure 7.39). One major difference between the seasonally-averaged spring and the May 1980 cluster structure was further discrimination of an estuarine embayment (Baker Bay and Youngs Bay trawl and beach seine collections) group. Although three regions were still evident among the station clusters, the May 1980 data indicated that the divisions between the demersal habitats and regions were located farther up the estuary. Bottom et al. (1984) suggested that this structure was the result of sharper depth stratification in the channel bottom habitats, with the bottom water extending farther upriver than during the winter. In contrast, in the water column and nearshore habitats the tidal-fluvial zone, coinciding with high river discharge, extended farther downriver than in the winter.

Station clusters from the low flow period (August 1980) indicated a similar division of the estuary into tidal-fluvial, estuarine mixing, and plume and ocean zones, but with the boundary between each situated more upriver than during the other two hydrologic seasons (Figure 7.40). Similar to the high flow cluster structure, incorporation of the FRI data further delineated a group of tidal flat (shallow embayment) stations, including trawl and beach collections in Baker and Youngs Bays and two collections from demersal slope and tidal flat habitats on Desdemona Sands.

Station groups identified using the fluctuating flow (January 1981) data indicated three demersal (trawl) groups, three channel water column (purse seine) groups, and two demersal (beach seine) groups which overlapped to form three general regions: (1) a fluvial and upper estuary region including Grays Bay; (2) a central estuary region including Baker Bay; and (3) an entrance region (Figure 7.41).

The spatial distribution of taxa-life history assemblages through the estuary was compared using nodal analysis of constancy on data from the three months representing hydrologic seasons (Bottom et al. 1984). In addition to defining discrete fish assemblages in association with the three capture methods, correlations with habitats and regions of the estuary were also illustrated (Figures 7.42-7.44).

Nodal constancy appeared to be low during the high flow season when juvenile salmonids and other species and life history stages entered the estuary (Figure 7.42). A closely associated group including Pacific staghorn sculpin and starry flounder appeared in the middle and lower reaches of the estuary, with shiner perch and subyearling English sole. Another demersal assemblage characterized by prickly sculpin and peamouth occurred primarily in the upper estuary while two other demersal assemblages (Pacific tomcod, snake prickleback, butter sole, and yearling English sole; Pacific sand lance, speckled sanddab, subyearling shiner perch, and subyearling Pacific herring) were relatively isolated in the central region. A salmonid-dominated assemblage (subyearling and yearling chinook, yearling coho, steelhead trout, and threespine stickleback) was present in both water column and demersal habitats throughout the estuary. Several other water column fish assemblages (yearling and adult American shad; yearling longfin smelt, yearling Pacific herring, and surf smelt) were also distributed principally in the central region.

During the low flow season constancy appeared to be more homogeneous among habitats and regions (represented by August 1980; Figure 7.43). In addition, reduced distinction among demersal, epibenthic, and water column taxa in the assemblages suggested more mixing of assemblages across habitats under these conditions. The distribution of the subyearling Pacific staghorn sculpin-starry flounder demersal assemblage, which also included subyearling and yearling shiner perch, had expanded in constancy and distribution into the tidal-fluvial zone of the estuary; the only habitat in which they did not occur was the water column habitat of that region. Another demersal assemblage of subyearling and yearling longfin smelt, Pacific tomcod, snake prickleback, subyearling English sole, sand sole, and yearling starry flounder occurred prominently in the middle and lower region of the estuary. An epibenthic assemblage of subyearling chinook, peamouth, and threesprine stickleback was also very abundant in water column and demersal slope habitats in all regions. Assemblages with more limited distributions included yearling and adult American shad, subyearling and yearling Pacific herring, and surf smelt in lower and mid-estuary water column habitats; northern anchovy, whitebait smelt, spiny dogfish, and yearling English sole in demersal habitats of the lower estuary; and largescale sucker, prickly sculpin, and subyearling American shad in demersal slope habitats of the tidal-fluvial zone.

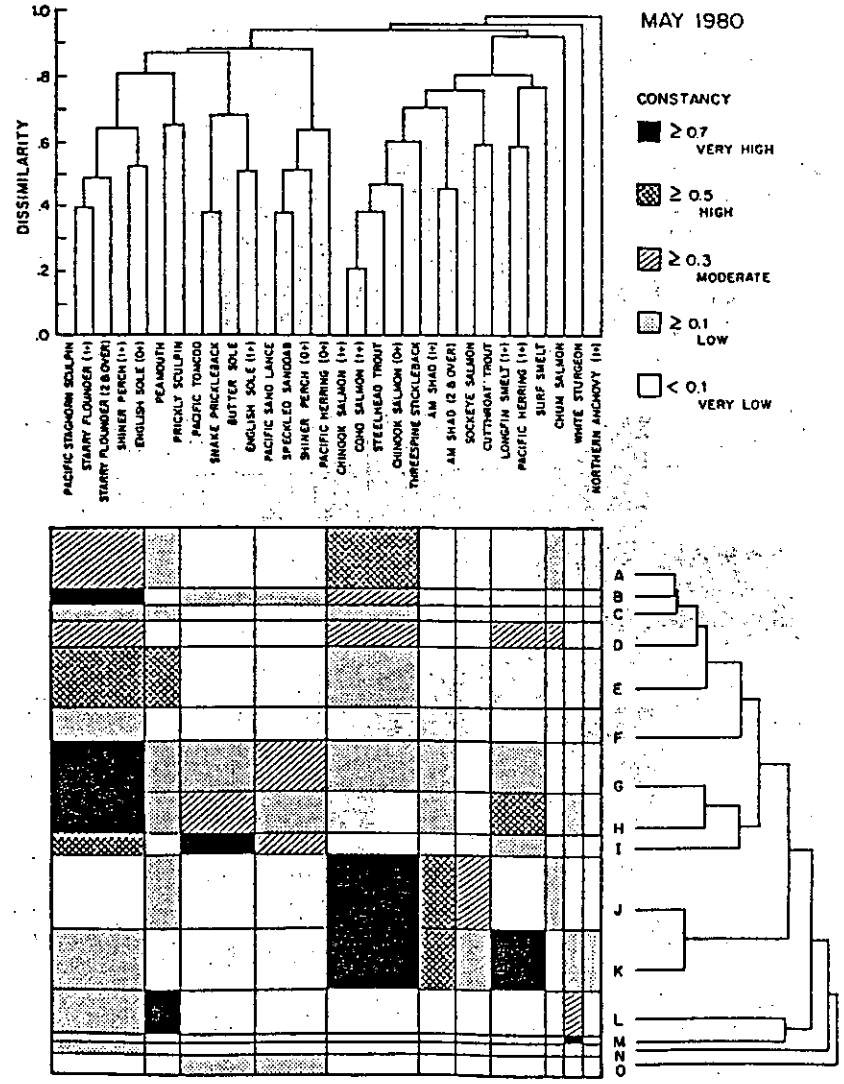


Figure 7.42. Nodal constancy of high flow (May 1980) taxa-life history and station clusters from CREDDP fish collections in the Columbia River Estuary.

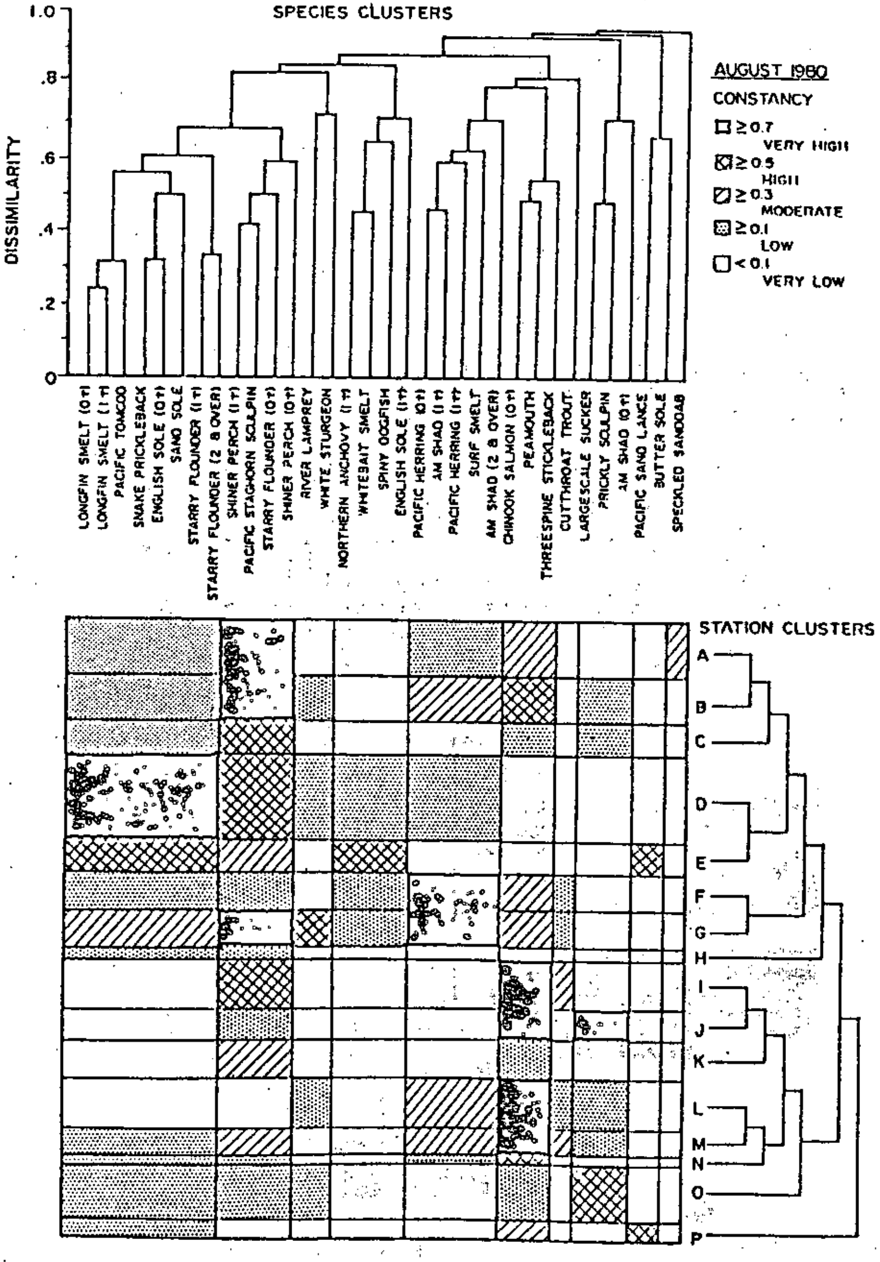


Figure 7.43. Nodal constancy of low flow (August 1980) taxa-life history and station clusters from CREDDP fish collections in the Columbia River Estuary.

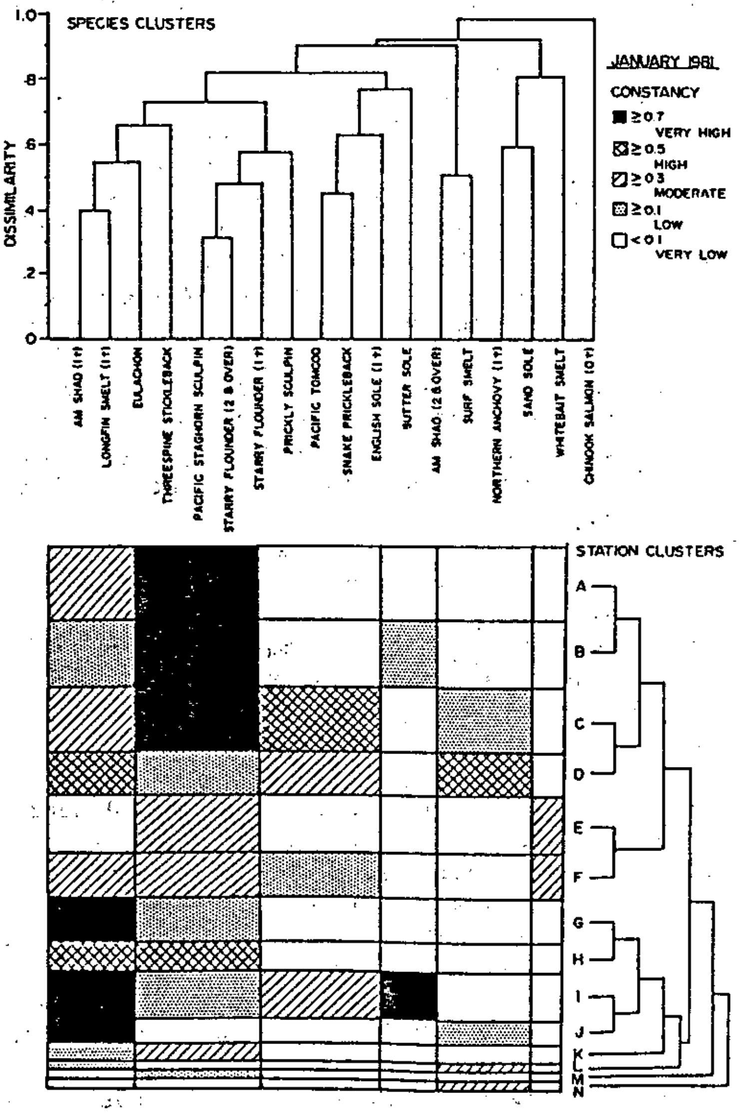


Figure 7.44. Nodal constancy of fluctuating flow (January 1981) taxa-life history and station clusters from CREDDP fish collections in the Columbia River Estuary.

During the fluctuating flow season (represented by January 1981 collections; Figure 7.44) two pelagic fish assemblages were distributed through the estuary: (1) a ubiquitous assemblage composed of yearling American shad, yearling longfin smelt, eulachon, and threespine stickleback, which tended to be most abundant in the middle and upper regions of the estuary; and (2) an assemblage of adult American shad and whitebait smelt occurring exclusively in the estuarine mixing zone. The ever-present assemblage of Pacific staghorn sculpin and starry flounder occurred with prickly sculpin predominantly in demersal slope habitats of the middle and upper areas of the estuary. Another demersal assemblage composed of Pacific tomcod, snake prickleback, yearling English sole, and butter sole was relatively confined to the estuarine mixing zone.

Results of discriminant analyses to statistically compare predicted group membership (based on cluster analyses) with actual group membership indicated that, although the clusters generally predicted groups correctly, the stations were more accurately represented as distributed along a continuum (Bottom et al. 1984). Reciprocal averaging ordination of the fish taxa-life history density data was also used to graphically illustrate differences among station and habitat associations and to elucidate the potential influence of environmental factors. The results of this analysis (Figures 7.45-7.47), again applied to three months' data representing the hydrologic seasons, supplied additional evidence of both the integrity of the more discrete taxa-life history assemblages as well as the continuum of stations along estuarine region and habitat gradients (Bottom et al. 1984).

Ordination of data from the high flow season showed station assemblages aligned along habitat and salinity gradients, with somewhat more distinct separation than in the fluctuating flow ordination (Figure 7.45a). Stations in water column and demersal slope habitats were separated into two--upper and lower--regions of the estuary with somewhat greater separation among the latter stations. The tidal flat and channel bottom (bottom trawl) stations illustrated broader zonation along the salinity gradient, with four groups ranging from a marine-lower estuarine group containing stations below Desdemona Sands to a purely fluvial group containing stations including and above Grays Bay. Tidal flat, demersal slope, and channel bottom habitat stations from the central region of the estuary ordinated into two distinct groups: (1) channel bottom stations between Desdemona Sands and Miller Sands; and (2) loosely associated demersal slope habitat stations in Baker and Youngs Bays combined with a very tight grouping of the channel bottom stations between Fort Stevens and Tongue Point. Taxa-life history stage ordinations from the high flow season indicated similar habitat and salinity gradients (Figure 7.46b). At least six to seven pelagic-epibenthic fish assemblages, characterized by a large, loosely ordinated group of juvenile salmonids and threespine stickleback, were ordinated along the center of the salinity gradient. Most of the demersal fish groupings were concentrated at the lower end (higher salinities) of the salinity gradient, except for the ubiquitous Pacific staghorn sculpin-starry flounder association, which was ordinated broadly along the middle-upper segment of this gradient.

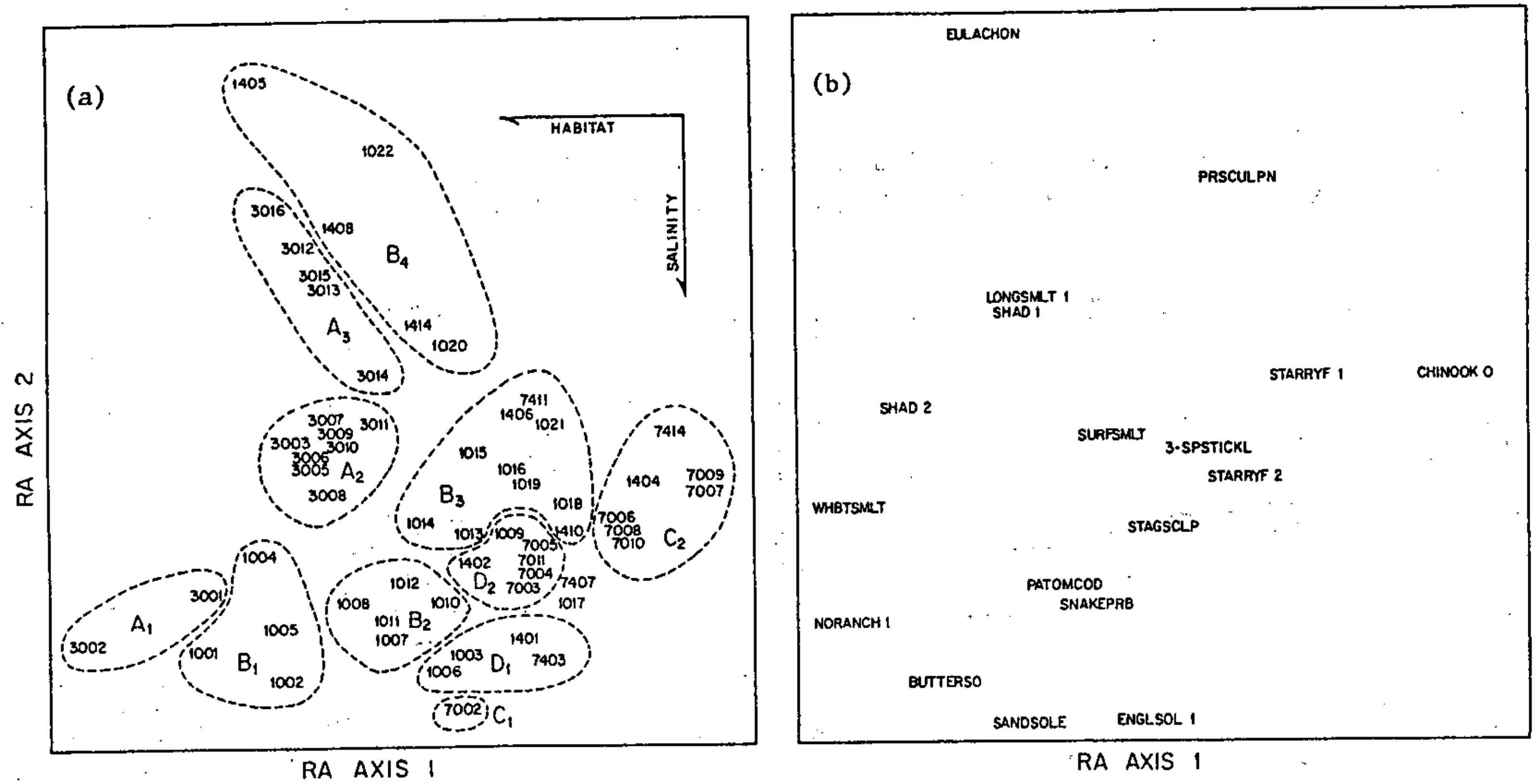


Figure 7.45. Reciprocal averaging plots by station (a) and taxa-life history stage (b) of CREDDP fish collections in the Columbia River Estuary during fluctuating flow season, January, 1981.

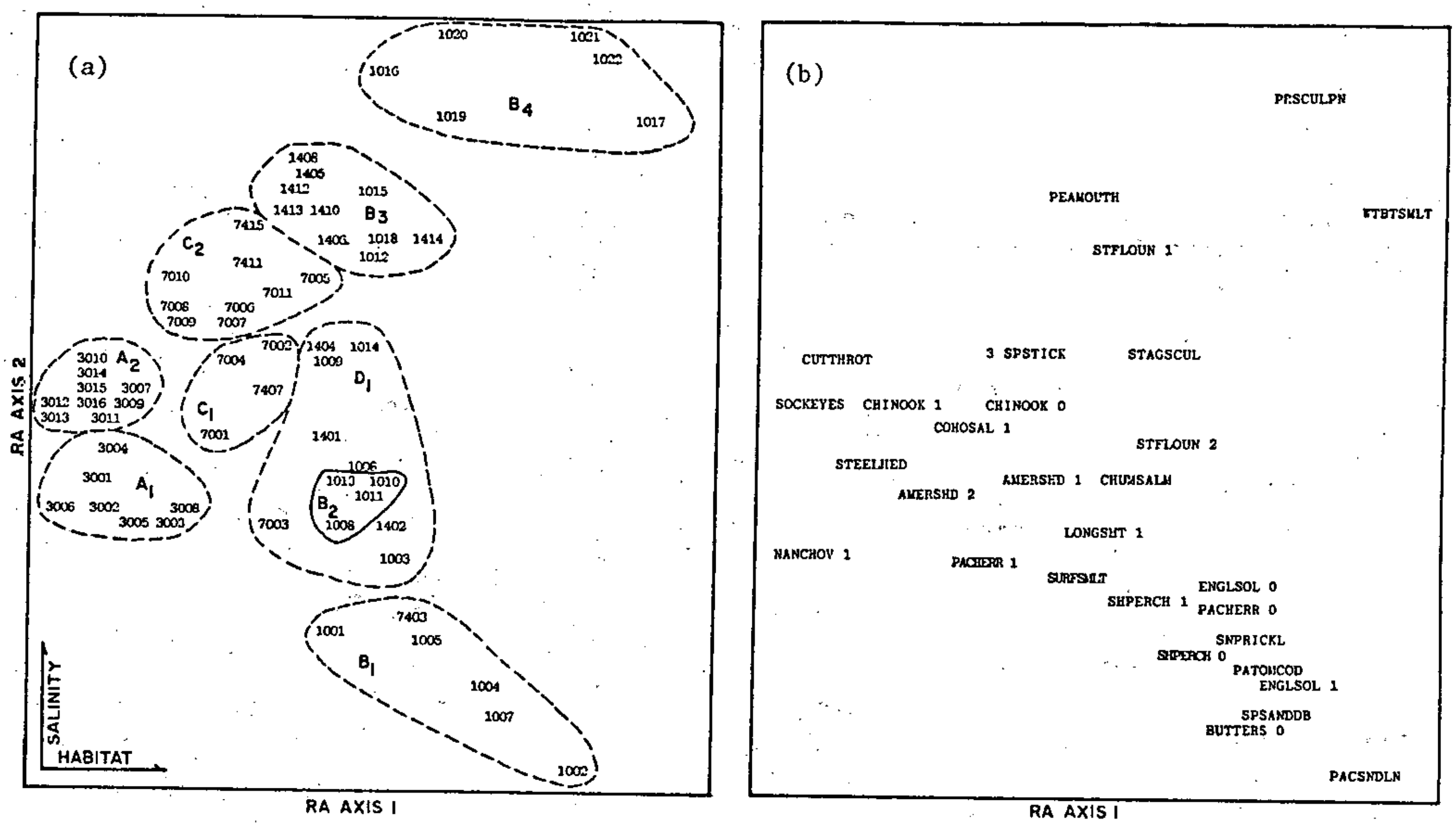


Figure 7.46. Reciprocal averaging plots by station (a) and taxa-life history stage (b) of CREDDP fish collections in the Columbia River Estuary during high flow season, May 1980.

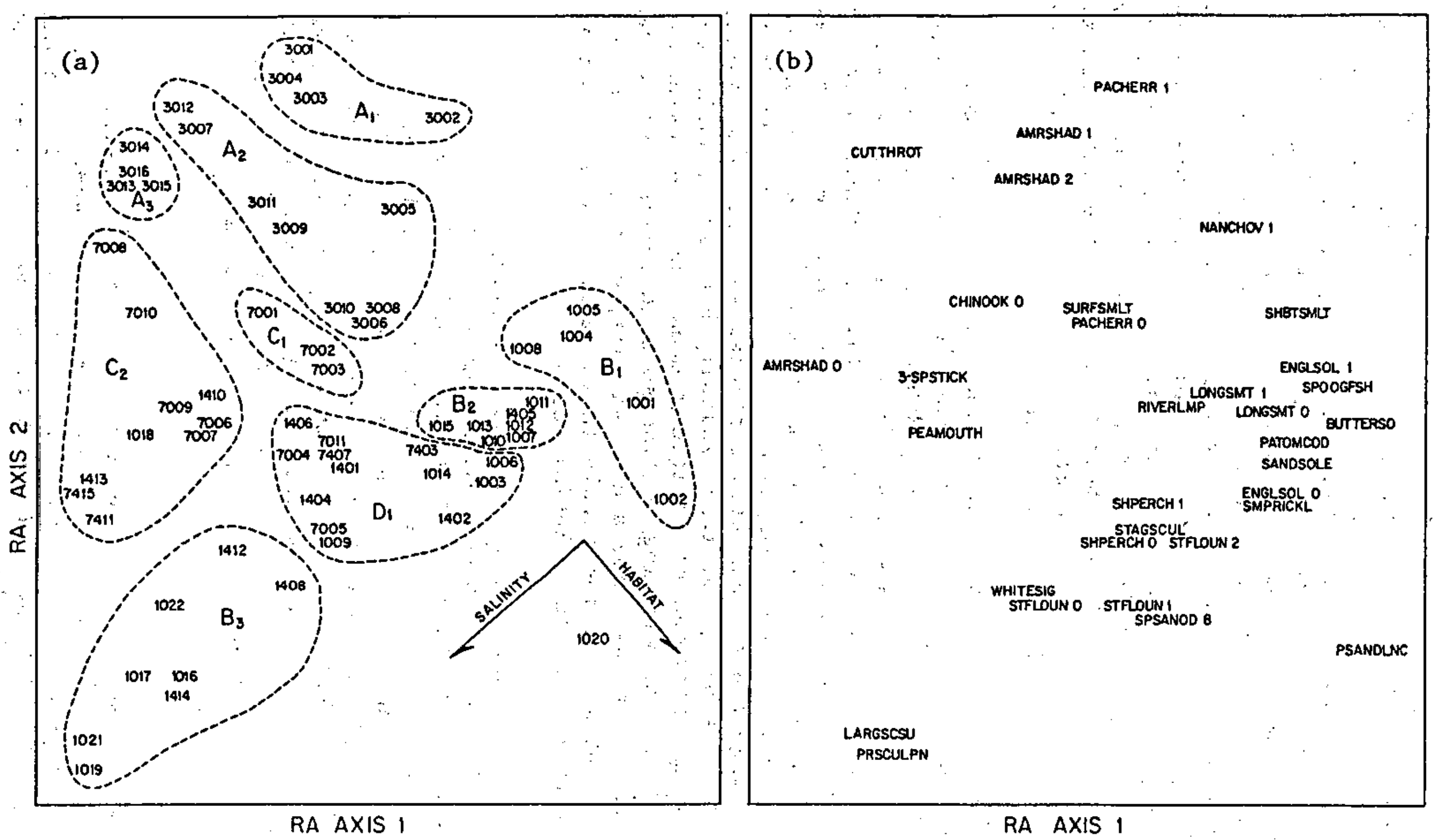


Figure 7.47. Reciprocal averaging plots by station (a) and taxa-life history stage (b) of CREDDP fish collections in the Columbia River Estuary during low flow season, August 1980.

Ordination of stations sampled during the low flow season produced much more diverse, dispersed groupings (Figure 7.46a) coincident with the increased mixing and salinity intrusion in the estuary during that hydrologic season (Chapter 3). Four pelagic fish groups were delineated, one each characterizing marine and fluvial regions and two in the mid to upper areas of the estuarine mixing zone. Demersal slope habitats were divided into two widely separated groups, one fluvial and one marine, and channel bottom habitats into three similar groups. A complex group of demersal slope and channel bottom stations from peripheral bays comprised a transitional group between the marine and fluvial extremes. Taxa-life history ordination also indicated more diversified groupings (Figure 7.46b). Two of the more closely associated groups included demersal fish from the central to upper reaches of the estuary: (1) Pacific staghorn sculpin, adult starry flounder, and shiner perch; and (2) English sole, snake prickleback, sand sole, Pacific tomcod, and longfin smelt. The pelagic and epibenthic fishes showed much lower association.

Stations sampled during the fluctuating flow season ordinated similarly along salinity and habitat gradients (Figure 7.47a). Pelagic and channel bottom stations separated into three salinity zones but only the plume and ocean zone stations were widely separated. Demersal slope stations also ordinated along a salinity gradient. Other distinct ordinations included five channel bottom stations with species composition similar to water column habitats in the fluvial region and tidal flat and demersal slope stations in Baker and Youngs Bays. Taxa-life history stage ordinations also reflected salinity and habitat influences (Figure 7.47b). Specific salinity-habitat associations included an assemblage composed of Pacific tomcod, snake prickleback, butter sole, sand sole, and yearling English sole in demersal slope and channel bottom habitats in the plume and ocean zone; subyearling chinook in demersal slope habitats in the tidal-fluvial zone; and eulachon in water column habitats in the tidal-fluvial region.

All of these multivariate analytical interpretations illustrate the strong role of the physical processes of mixing and salinity intrusion in structuring the composition, distribution, and integrity of the estuary's fish assemblages. In general, increased stratification and depressed salinity intrusion during the two seasons of periodically (late fall and winter) or constantly (spring) high river discharge permit or impose greater separation of assemblages. Decreased riverflow (summer and early fall), which promotes mixing and expanded salinity intrusion, expands the habitats available for the truly estuarine assemblages and, in the process, contributes to their disassociation.

Avifauna

In terms of frequency of occurrence and mean density, the predominant avian predators in the estuary were the western grebe (Aechmophorus occidentalis); double-crested cormorant (Phalacrocorax auritus); hybrid gulls (Larus spp.); a multispecies shorebird assemblage (collectively termed "peeps" due to the difficulty of separately enumerating them at high densities and because of their similar feeding modes) composed of sanderling (Calidris alba), dunlin (C. alpina), and western sandpiper (C. mauri); common crow (Corvus corax); common merganser (Mergus merganser); surf scoter (Melanitta fusca); and great blue heron (Ardea herodis).

Coincident with their seasonal migrations, western grebes were reported throughout the estuary (Figure 7.48a), but aggregations related to feeding activities were specifically observed in shallow habitats between Point Ellice and Knappton Point and in the region of Karlson Island and Youngs Bay in the spring, and in the vicinity of Tongue Point and from Knappton Bay to Harrington Point during the winter (Hazel et al. 1984). As residents, double-crested cormorants were more uniformly distributed seasonally and spatially in the estuary (Figure 7.48b). Their occurrence related to both nesting as well as feeding sites, and particularly to structures such as pile dikes which are utilized as drying (of feathers after diving for prey) sites near feeding areas. In particular, areas near Tongue Point, between Miller Sands and Karlson Island, between Harrington Point and Jim Crow Point, west of Wauna, and near Nassa Point were interpreted as valuable feeding areas. Hybrid gulls were distributed ubiquitously through the estuary during all seasons, with habitat and area utilization varying according to nesting, feeding, and loafing activities (Figure 7.48c). In general, channels, tidal flats, and marshes in all regions of the estuary were used for feeding by hybrid gulls.

Peeps were exceptionally prominent in the estuary only during their spring and fall migrations along the Pacific flyway, although numerous peeps overwintered in the system (Figure 7.49a). When in the estuary, they foraged exclusively on tidal flats and adjoining marshes, particularly in association with ebb tide periods. Although commonly perceived as a terrestrial species, common crow were ubiquitous and often abundant in tidal flat, marsh, and swamp habitats in the estuary (Figure 7.49b); feeding activity was observed specifically in tidal flat and marsh habitats. Common merganser occurred almost exclusively above Tongue Point and, although observed during all seasons, were most common during spring and appeared aggregated during the winter (Figure 7.49c). Concentrated feeding activities occurred during tidal inundation of demersal slope and tidal flat habitats between Knappton Bay and Harrington Point and in the vicinity of Karlson Island.

Surf scoter occupied open water habitats in the central and lower reaches of the estuary during winter and spring (Figure 7.50a), although feeding did not occur in any particular habitat. Great blue herons maintained resident populations in the estuary, with concentrations associated with specific nesting and foraging areas (Figure 7.50b). Most of the heron concentrations in the central region of the estuary were associated with nesting sites (heronries). Feeding activities were distributed more homogeneously over tidal flat and marsh habitats, with feeding most often observed in the shallow waters of the peripheral bays (Baker, Youngs, and Grays) and throughout the Cathlamet Bay region between Tongue Point and Tenasillahe Island.

Terrestrial Wetland Mammals

Terrestrial-wetland predators (tertiary consumers) included the

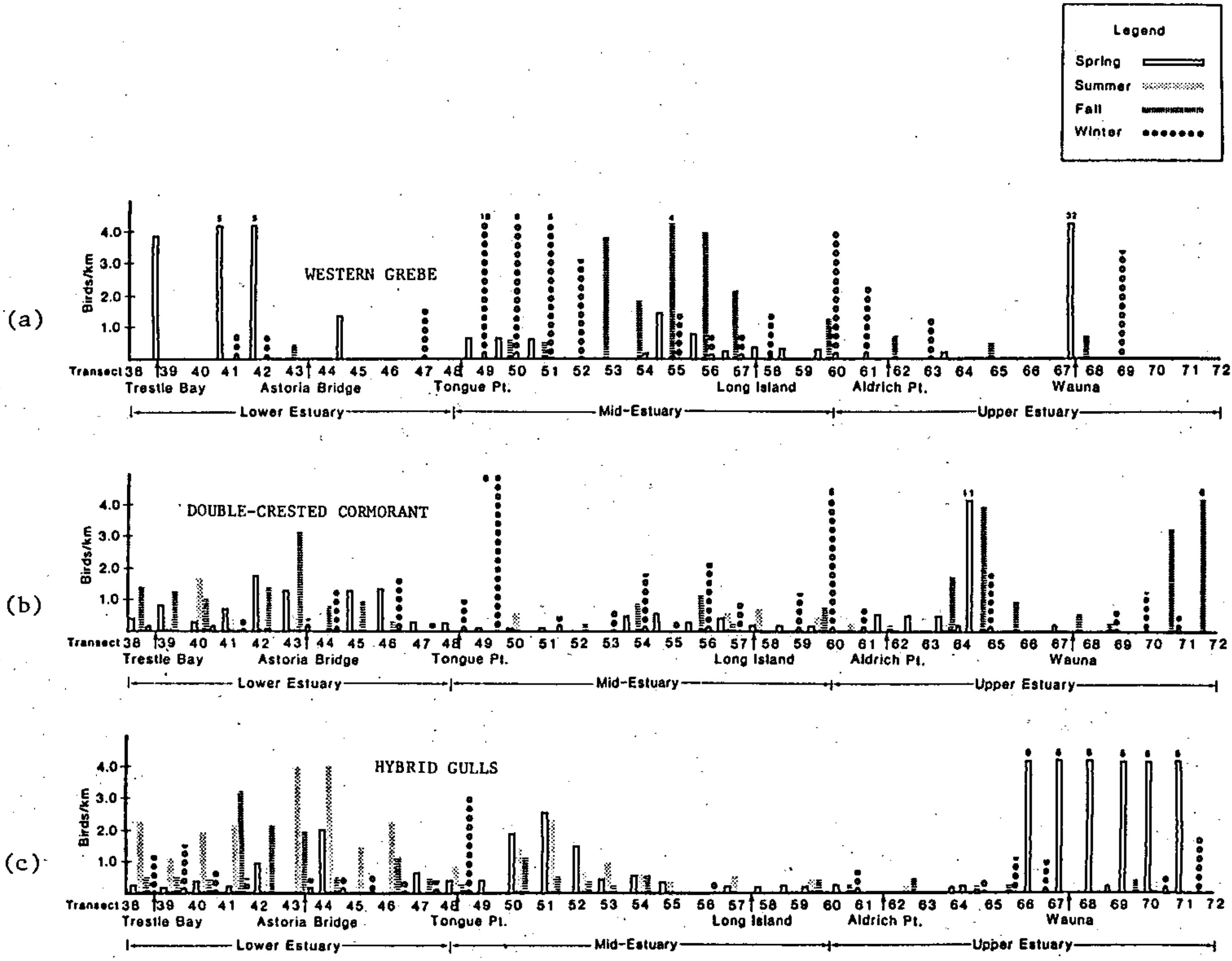


Figure 7.48. Distribution and relative abundance (birds/km) of western grebes (a), double-crested cormorants (b), and hybrid gulls (c) in the Columbia River Estuary during 1980 and 1981 (Hazel et al. 1984).

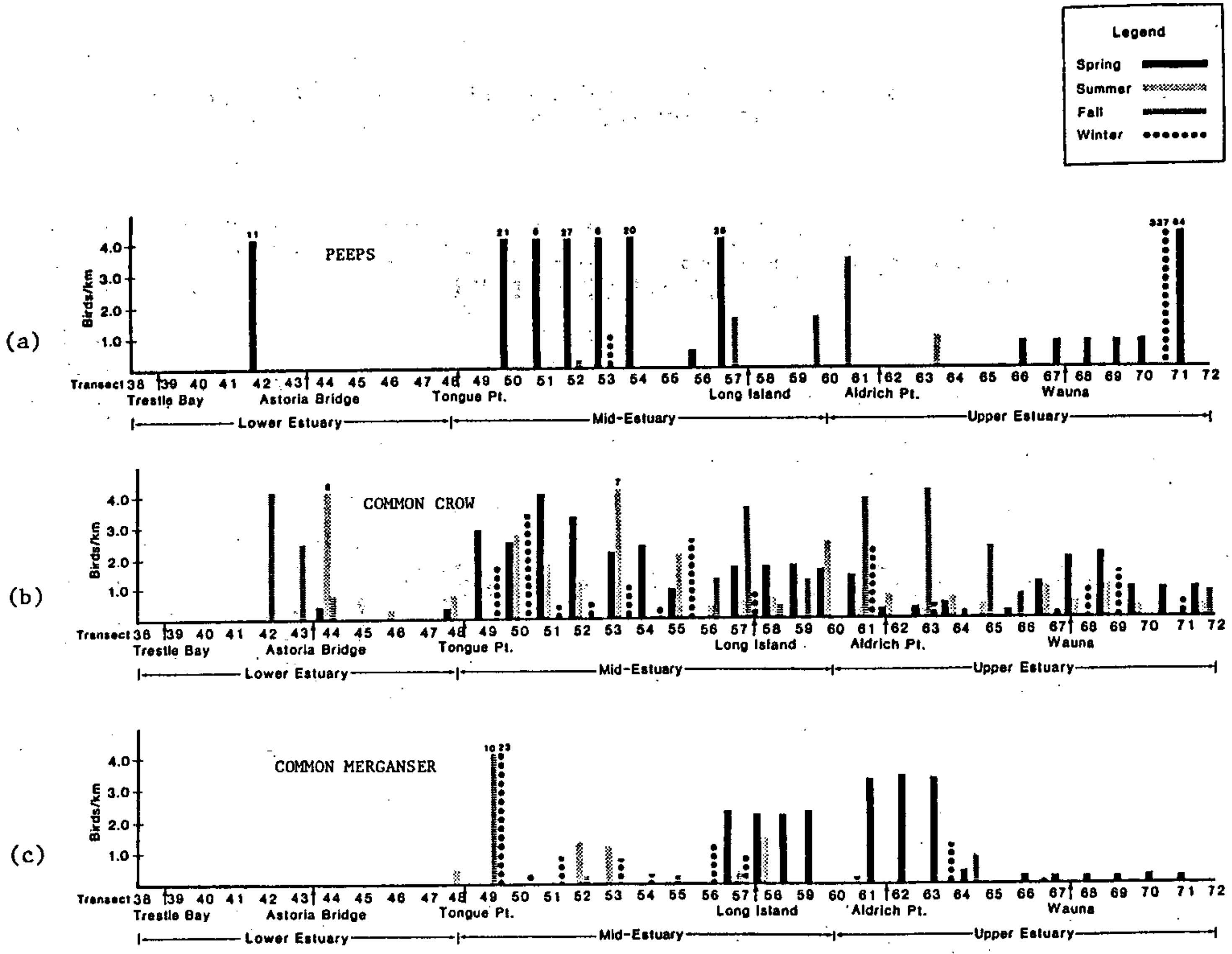


Figure 7.49. Distribution and relative abundance (birds/km) of peeps (a), common crows (b), and common mergansers (c) in the Columbia River Estuary during 1980 and 1981 (Hazel et al. 1984).

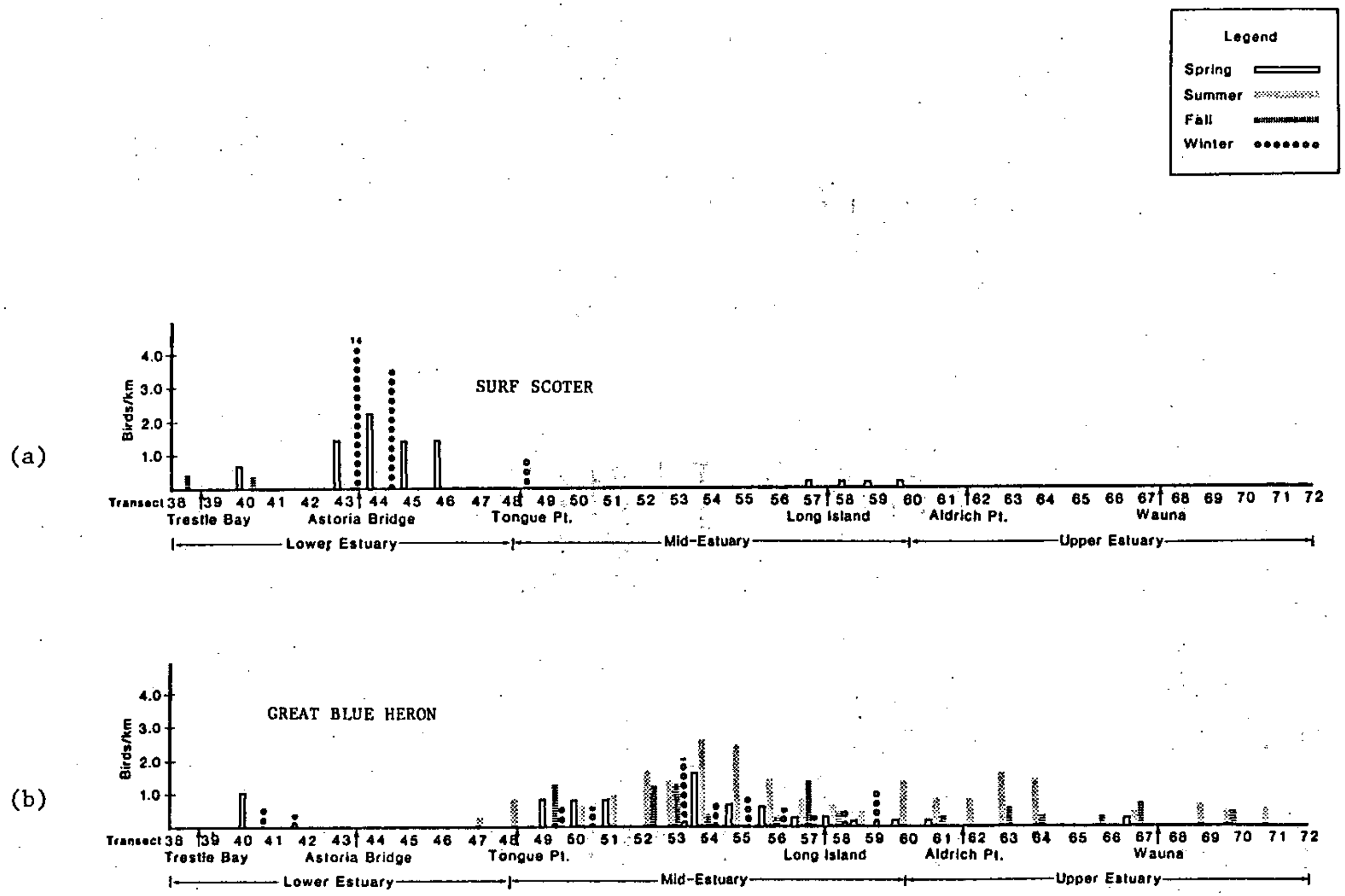


Figure 7.50. Distribution and relative abundance (birds/km) of surf scoters (a) and great blue herons (b) in the Columbia River Estuary during 1980 and 1981 (Hazel et al. 1984).

Canadian river otter (*Lutra canadensis*) and the raccoon (*Procyon lotor*); the vagrant shrew (*Sorex vagrans*), by its foraging upon insects, was classified as a predator at the secondary consumer level. Canadian River otters were observed along tidal channels in swamp, marsh, and tidal flat habitats throughout the estuary (Figure 7.51) and were particularly associated with Sitka spruce habitats. Canadian river otters were particularly common at Baker, Youngs, and Grays Bays and the complex island habitat of Cathlamet Bay and the Fluvial Region. Raccoons occurred in a similar shoreline distribution to the otters but were more common among the islands in the upriver reaches of the tidal-fluvial zone (Figure 7.51). Both swamp (orange balsam and Sitka spruce habitats) and marsh (Lyngby's sedge/cat-tail habitat) indicated high occurrences of raccoon feeding activity. The vagrant shrew was very common in swamp and marsh habitats over the whole estuary.

Marine Mammals

All four marine mammals common to the estuary--northern sea lion (*Eumetopias jubata*), California sea lion (*Zalophus californianus*), harbor seal (*Phoca vitulina richardi*), and northern elephant seal (*Mirounga angustirostris*)--were classified as tertiary consumer level predators.

Maximum occurrence of both California and northern sea lions within the region of the estuary, as indexed by the South Jetty haulout populations, increased steadily from September until mid-winter (e.g., December-February for northern sea lions, March for California sea lions) and then declined until June (Figure 7.52). Adult Pacific harbor seals also showed some temporal and spatial variation over the same period, but appeared to maintain between 100 and 800 in the estuary throughout the year, which averaged 465 animals per month (Table 7.35). A seasonal maximum was still evident between December and April, principally because of increases in the number of seals occupying the haulout areas at Wallace Island, Taylor Sands, and Miller Sands. But the haulout at Desdemona Sands was constantly inhabited by over 100 seals and the haulout at Green Island was occupied only during the summer.

7.3.3 State Variables

Wetland Herbivory

Merker and Fenton (1984) estimated population densities of wetland herbivorous mammals (Table 7.36). Densities range broadly from 0.02-0.06 animals ha^{-1} (estuarine populations of 38-109) for Columbian white-tailed deer to 2.5-20.8 ha^{-1} (estuarine population estimates of over 1 x 10^{5}) for nutria. Corresponding standing crop estimates range between minima of 0.07-0.09 kgC ha^{-1} for muskrat and Columbian white-tailed deer to a maximum of 9.8 kgC ha^{-1} for nutria. These estimates indicate that, exclusive of the small mammal (deer mouse, Townsend's vole, vagrant shrew) populations which were unassessed, between 745 and 780 MT C of wetland herbivores occupy the Columbia River Estuary; the small individual size of the unestimated herbivores suggests that this estimate would not change dramatically with their

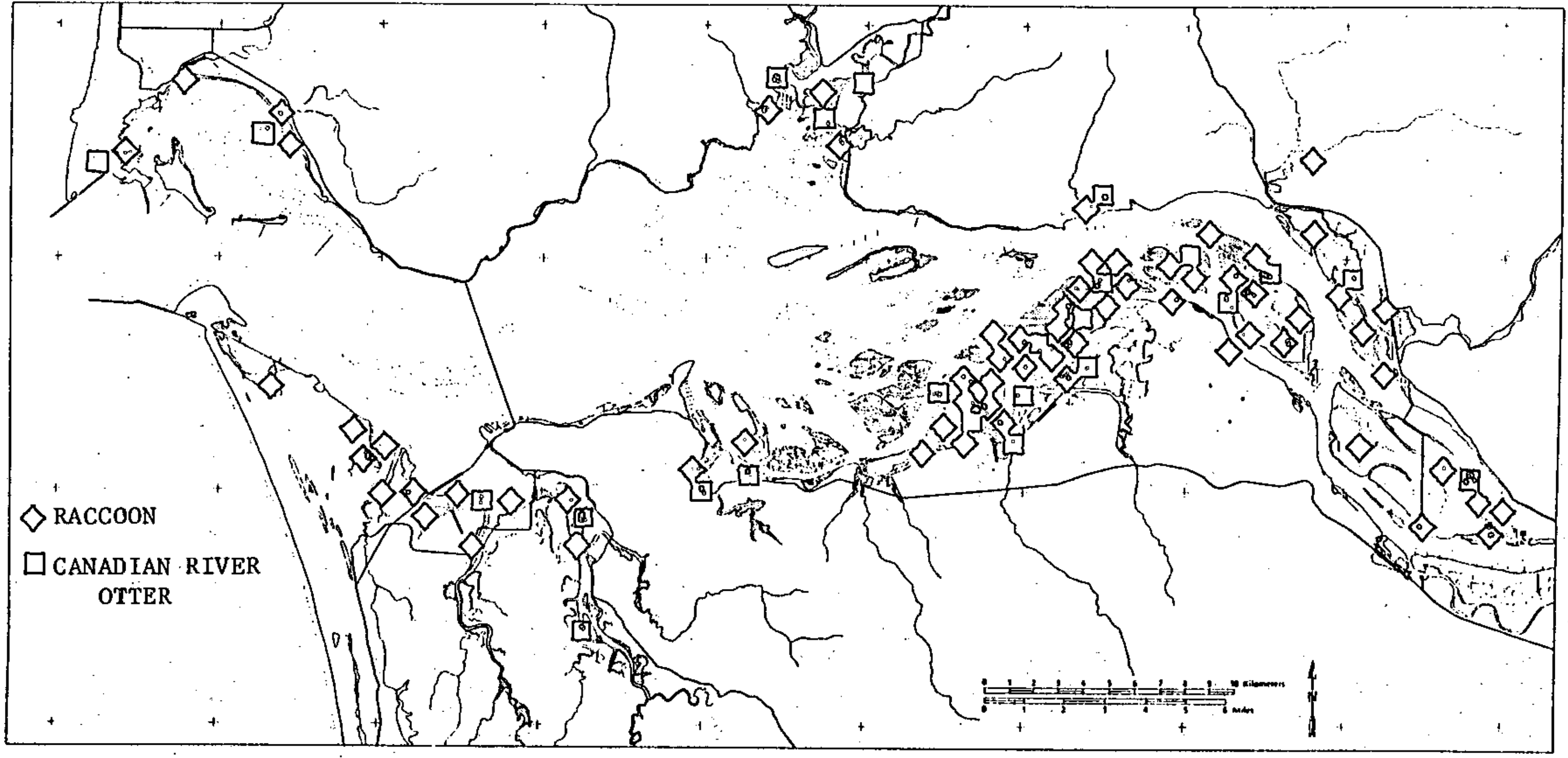


Figure 7.51. Distribution of predatory aquatic mammals utilizing wetland habitats of the Columbia River Estuary during CREDDP studies, 1980-1981. Symbols indicating locations of raccoon and Canadian river otter are representational; see Dunn et al (1984) for more exact locations.

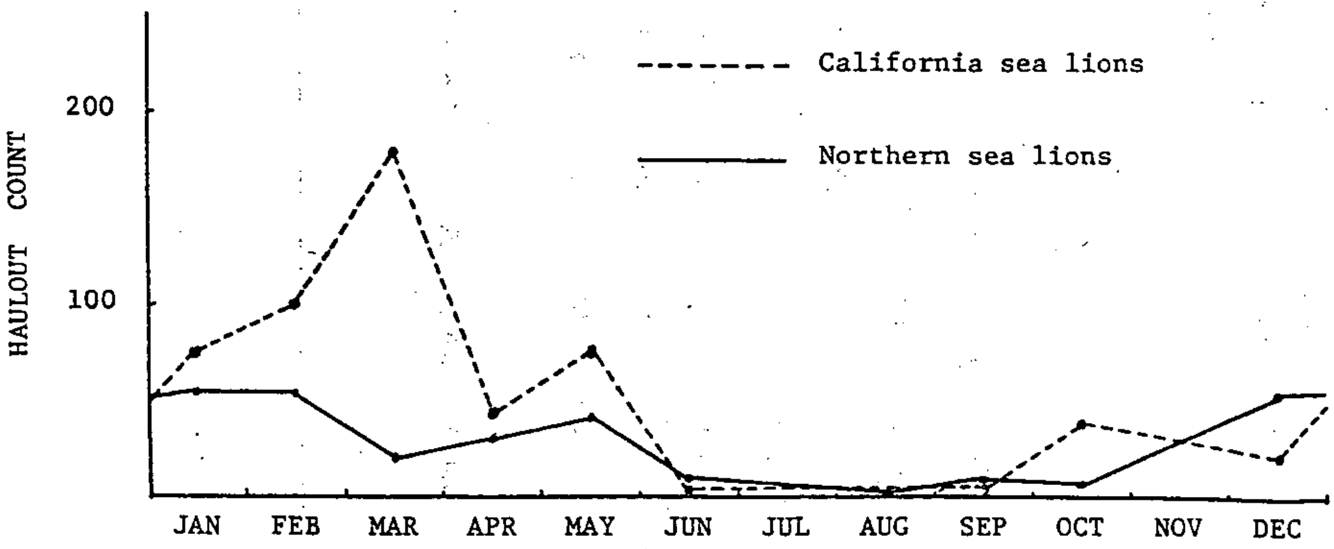


Figure 7.52. Seasonal occurrence of California and northern sea lions at the south jetty, Columbia River (Maximum counts, 1980 to 1982) (Jeffries et al. 1984).

Table 7.35. Average monthly aerial counts of adult harbor seals at nine haulout locations in the Columbia River Estuary, April 1980 - September 1982.

HAULOUT LOCATION	MONTH											
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
South Jetty	0	NS	1	0	0	0	0	1.0	1.0	0		0
Baker Bay	NS	NS	NS	4.0	0.3	0	0	3.5	5.5	14.7	NS	0
Desdemona Sands	319.5	NS	264	486.3	317.7	145.4	355.1	300.3	346.3	123.5	NS	301
Taylor Sands	241.8	NS	548	101.3	0.5	0.7	9.0	0	9.3	46.0	NS	174
Grays Bay	0.3	NS	0	0	1.2	4.0	3.3	0	5.3	0	NS	0
Miller Sands	210.5	NS	82	56.8	2.7	1.0	0	0	0	6.0	NS	46
Green Island	0	NS	0	0	1.0	0	35.3	33.5	21.7	0	NS	0
North Woody Island	43.3	NS	3	3.0	0	NS	NS	0	NS	0	NS	0
Wallace Island	94.7	NS	0	17.5	0	NS	NS	NS	NS	NS	NS	NS
Monthly Mean Total	889.8	NS	896.0	657.0	320.8	146.8	375.7	326.0	365.2	159.0	NS	521.0

NS = NOT SURVEYED

Table 7.36. Population standing stock of wetland herbivorous and predatory mammals in Columbia River Estuary (Merker and Fenton 1984).

CATEGORY	TAXA	ESTIMATED STANDING STOCK DENSITY (no. ha^{-1})	STANDING CROP ((kgC ha^{-1})
HERBIVORES	Nutria	2.5-20.8	1.01-9.80
	Muskrat	0.75-6.6	0.07-0.66
	American Beaver	0.3	0.32
	Columbia White-tailed Deer	0.02-0.06	0.09-0.26
	Columbia Black-tailed Deer	0.08	0.34
PREDATORS	Raccoon	0.08	0.02
	River Otter	0.02	0.02

inclusion. There is no information on seasonal changes in standing stock, which probably changes during winter-spring, when animal movement, hibernation, and reproduction activities are at a peak.

Deposit Feeding

Benthic Infauna

Information on the state variable for benthic infaunal deposit-feeders was obtained from the results of the September 1981 distributional survey of benthic infauna (Holton et al. 1984).

Considering benthic infauna generally, regardless of feeding mode, within the context of assemblage structuring by broad salinity and habitat characteristics (see Section 7.3.2), standing crop (mgC m^{-2}) was found to be closely related to sediment structure (Holton et al. 1984). The most important sediment characteristics were the fraction of fine (less than 0.063 mm) particles and the percent organic content (determined by combustion) which were positively correlated (Figure 7.53). The relationship between benthic infauna standing crop and both sediment fines fraction (Figure 7.54) and organic content (Figure 7.55) indicated significant relationships. In both cases, benthic infauna standing crop was generally higher in finer, more organic sediments. These sediments are more characteristic of the lower-energy peripheral bays (Baker, Trestle, Youngs, Grays, Cathlamet) than tidal flat habitats in the tidal-fluvial zone or mid-estuary. Both characteristics decrease with increasing depth into demersal slope and channel bottom habitats.

This relationship is particularly germane to deposit feeders, which feed on surface deposits of detritus and living organic matter and require less energetic, more depositional and organic environs to maintain their populations. Thus, partitioning of benthic infauna standing crop by taxa feeding mode and estuarine habitats (reflecting sediment structure) and region (reflecting position and salinity regime in estuary) indicate that peripheral bays in the lower estuary sustain higher standing crops of deposit-feeding benthic infauna than comparable habitats upriver in the estuary or more coarse-grained, less-organic habitats in the same area (Table 7.37; see Table 8.3 for related data). In extreme cases, there is almost an order of magnitude difference between tidal flats in the estuarine mixing zone (about 3,487 mgC m^{-2} in Baker and Trestle bays) and those in the tidal-fluvial zone (410-456 mgC m^{-2} in Grays Bay and fluvial region tidal flats). Not surprisingly, the lowest standing crops of deposit-feeding infauna occurred in the high-energy, coarse-grained habitats of all channel bottoms (about 46-61 mgC m^{-2}) and demersal slopes in the central region of the estuary.

Although seasonal data for deposit-feeding benthic infauna assemblages was not available from the distributional survey data, populations of prominent deposit-feeders were monitored over a 14-month period at the Baker Bay intensive study site (Holton et al. 1984). Average density for the deposit-feeding assemblage over the study period was 20,310 organisms m^{-2} and standing crop was about 4.7 gC m^{-2}, with oligochaetes dominating (53%) the density and Macoma balthica (89%) the standing stock (Table 7.38). Densities were variable seasonally,

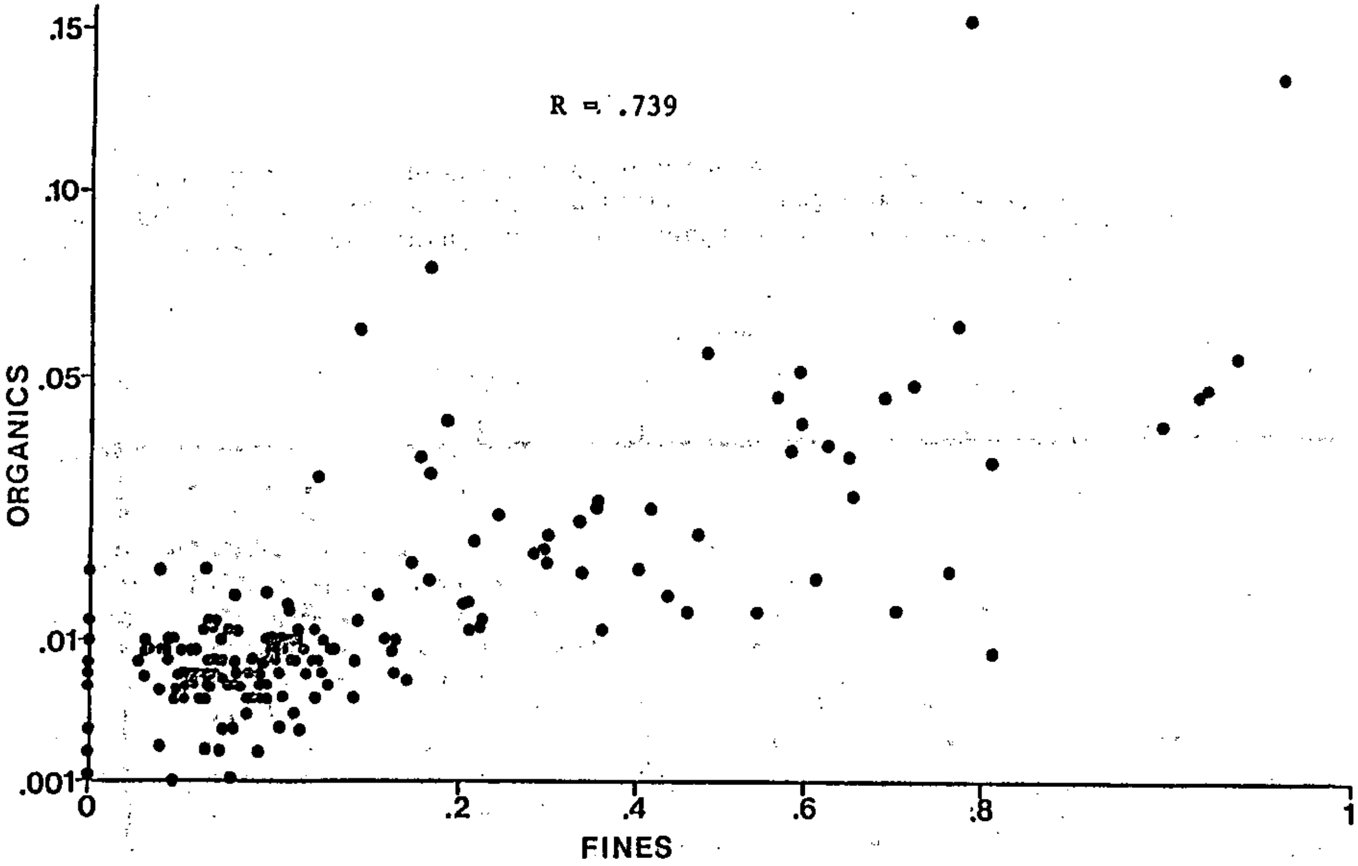


Figure 7.53. Scatterplot of sediment organic content and fines fraction for all stations in distributional survey of benthic infauna in the Columbia River Estuary, September 1981 (Holton et al. 1984).

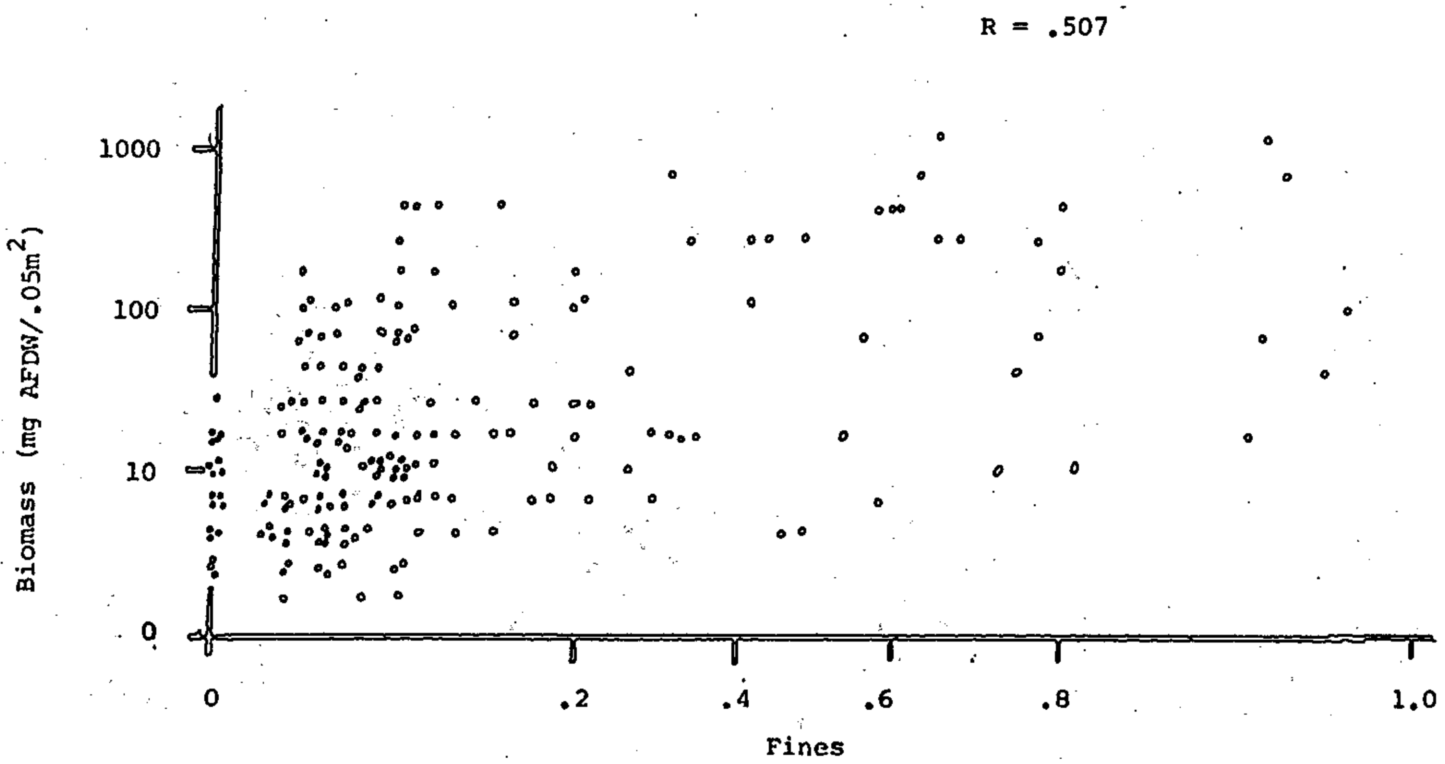


Figure 7.54. Scatterplot of benthic infauna standing crop and sediment fines fraction for all stations in distributional survey of the Columbia River Estuary, September 1981 (Holton et al. 1984).

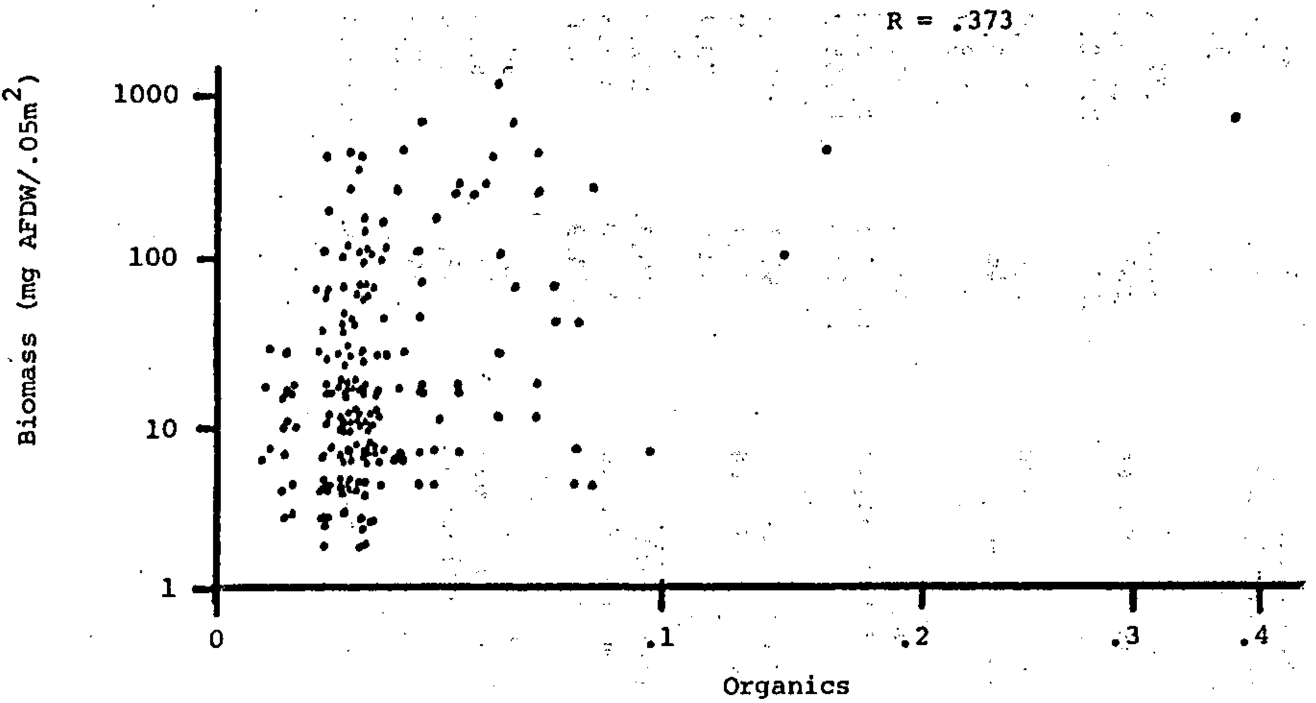


Figure 7.55. Benthic infauna standing crop and sediment organic fraction for all stations in distributional survey of the Columbia River Estuary, September 1981 (Holton et al. 1984).

Table 7.37. Standing crop (mgC m^{-2}) of deposit-feeding benthic infauna in different regions and habitats of the Columbia River Estuary (Data from D. Higley and R. Holton, OSU; Unpubl.).

REGION	HABITAT	STANDING CROP (mgC m^{-2})	
		mean	± Standard
ENTRANCE	Tidal Flats	63.1	83.0
	Channel Bottom	60.5	78.5
Region Subtotal		61.0	77.1
BAKER-TRESTLE BAYS	Tidal Flats	3,486.6	2,728.4
	Demersal Slopes	2,285.2	2,778.4
Region Subtotal		3,225.5	2,722.6
ESTUARINE CHANNELS	Demersal Slopes	357.4	824.3
	Channel Bottom	46.3	43.7
Region Subtotal		201.9	598.7
YOUNGS BAY	Tidal Flats	652.4	254.1
	Demersal Slopes	1,462.5	1,922.6
Region Subtotal		1,012.5	1,265.2
MID-ESTUARY SHOALS	Tidal Flats	91.1	110.5
	Demersal Slopes	28.1	15.9
Region Subtotal		50.0	70.7
GRAYS BAY	Tidal Flats	410.7	282.2
	Demersal Slopes	417.0	396.3
Region Subtotal		413.9	328.0
CATHLAMET BAY	Tidal Flats	222.1	390.0
	Demersal Slopes	66.8	69.8
	Channel Bottom	46.6	84.9
Region Subtotal		134.6	240.5
	TOTAL ALL REGIONS	569.4	1,424.3

Table 7.38. Deposit-feeding benthic infauna retained on a 0.5 mm screen from Baker Bay mudflat intensive study site. Density and standing crop are expressed as average values for the study period. NW - insignficant weight.

TAXA	DENSITY (m^{-2})	STANDING CROP (mgC m^{-2})
Oligochaete	10,745	96
Hobsonia florida	3,162	133
Pseudopolydora kempi	2,744	165
Macoma balthica	2,182	4,149
Hemileucon sp.	412	5
Turbellaria	366	16
Neanthes limnicola	227	47
Mediomastus spp.	155	2
Pygospio elegans	104	1
Corophium salmonis	79	8
Rhynchocoela	60	7
Myidae sp.	25	
Heteromastus spp.	21	28
Eogammarus confervicolus	11	1
Paraphoxus milleri	4	1
Gnorimosphaeroma oregonensis	2	N/W
Crangonidae (juvenile)	7	N/W
Decapoda (larvae)	4	N/W
TOTAL	20,310	4,657

however, for all taxa except the infaunal bivalves (Figure 7.56). In most cases, peak densities occurred during the low flow period, July through September.

From the standpoint of its ubiquitous distribution and abundance, as well as its importance as a food organism for higher level consumers such as juvenile salmon, one of the most important deposit-feeding infaunal organisms in the estuary is the tubiferous amphipod *Corophium salmonis* (Holton et al. 1984). More detailed population structure studies were conducted on populations of this species at two very different tidal flat habitats, the peripheral embayment at Grays Bay with a seasonally-high deposition of fine sediments and the exposed mid-estuary shoals at Desdemona Sands with coarser-grained sediments (Holton et al. 1984). Such contrasting benthic environments were reflected in the density distributions at the two sites over the 12-month study period (Figure 7.57). While densities at Desdemona Sands (Figure 7.57a) disappeared between September 1980 and April 1981, they built up to a (mean) maximum of 96,096 m^{-2} by August 1981. This rapid increase in density on the shoals appears to have been due principally to the recruitment of juveniles from both the spring and fall generations. In contrast, the population at Grays Bay (Figure 7.57b) was considerably more stable, increasing steadily throught the winter from a mean of 9,741 m^{-2} in August 1980 to a maximum of 31,754 m^{-2} in February 1981 and declining again to a minimum of 4,122 m^{-2} in July 1981. Differences in both magnitude and temporal distribution of the Grays Bay *Corophium* densities may be due to the life history composition of the animals recruited to the population, which were adults or immature individuals rather than juveniles. Thus, the demography of the population and the seasonal structure and stability of the sedimentary environment are all important determinants to the standing stock of deposit-feeding benthic infauna.

Epibenthic Zooplankton

Approximately half of the epibenthic zooplankton taxa were considered to be deposit feeders. Accordingly, densities over all ten sampling sites in the estuary averaged 18,805 organisms m^{-2} and ranged between 95 and 40,000 m^{-2}; the 95% confidence interval of the density estimates was 11,210 to 26,400 m^{-2}. Density values approximated a negative binomial distribution and a median value of 5,204 m^{-2} (Simenstad 1984). Densities were quite variable among the three habitats (tidal flats, demersal slopes, channel bottoms), with the highest densities occurring in tidal flat habitats (mean +/- one standard deviation of 21,809+/-4,671 m^{-2}) compared to demersal slopes (12,562+/-4,180 m^{-2}) and channel bottoms (9,996+/-3,242 m^{-2}).

Seasonality in epibenthic zooplankton density also varied among habitats over the 18-month sampling period (Figure 7.58). Except for unusually high densities at the Astoria-Megler Bridge in October 1980 and Baker Bay in April 1981, densities at the five tidal flat sites (Figure 7.58a) consistently showed maxima in May and July-August, winter minima, and gradually increased from April to July 1981. Densities in demersal slope habitats (Figure 7.58b) generally exhibited only one summer (August) maximum except for a spring (April-May) peak at the

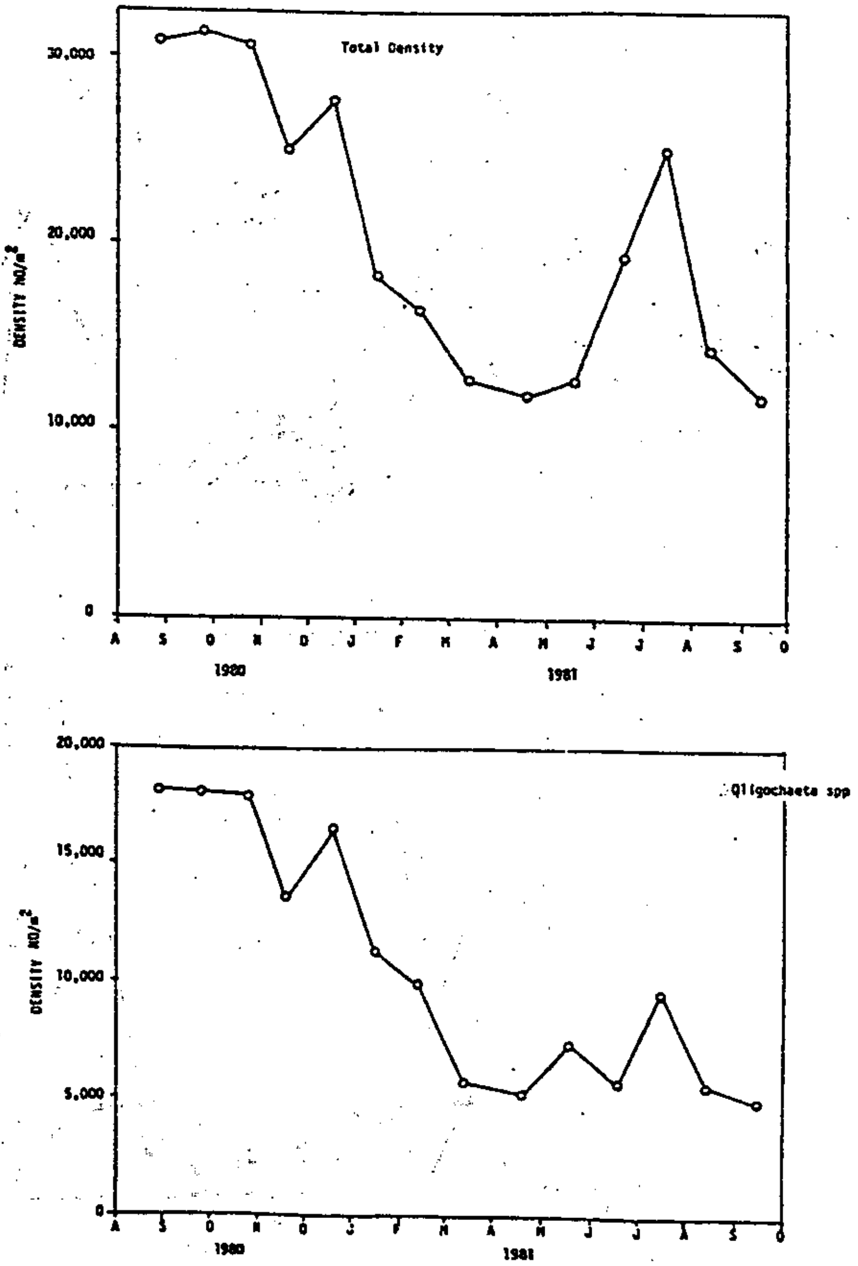


Figure 7.56. Monthly changes in total density and density of deposit feeding benthic infauna at Baker Bay intensive study site, August 1980 - September 1981 (Holton et al. 1984).

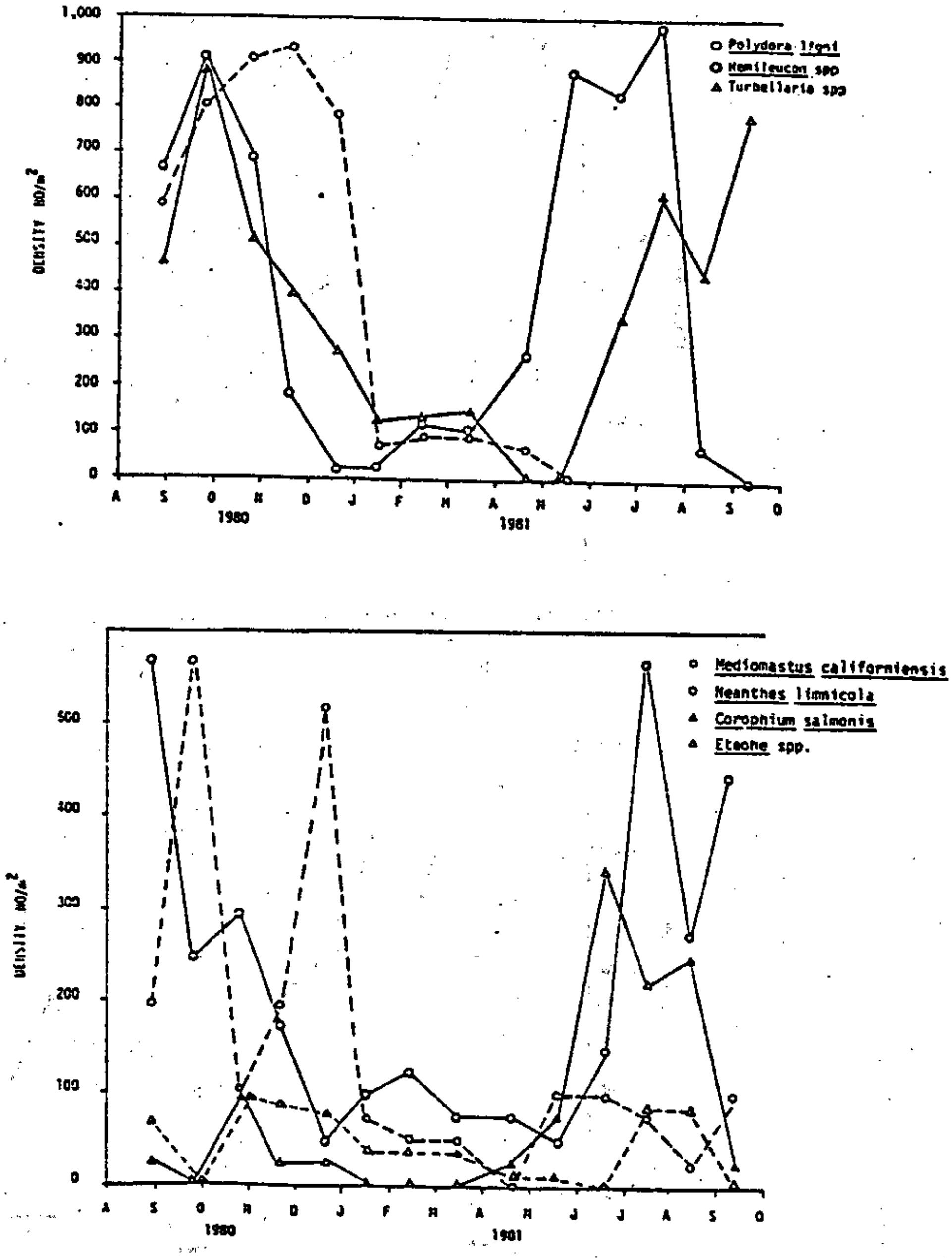


Figure 7.56 (continued).

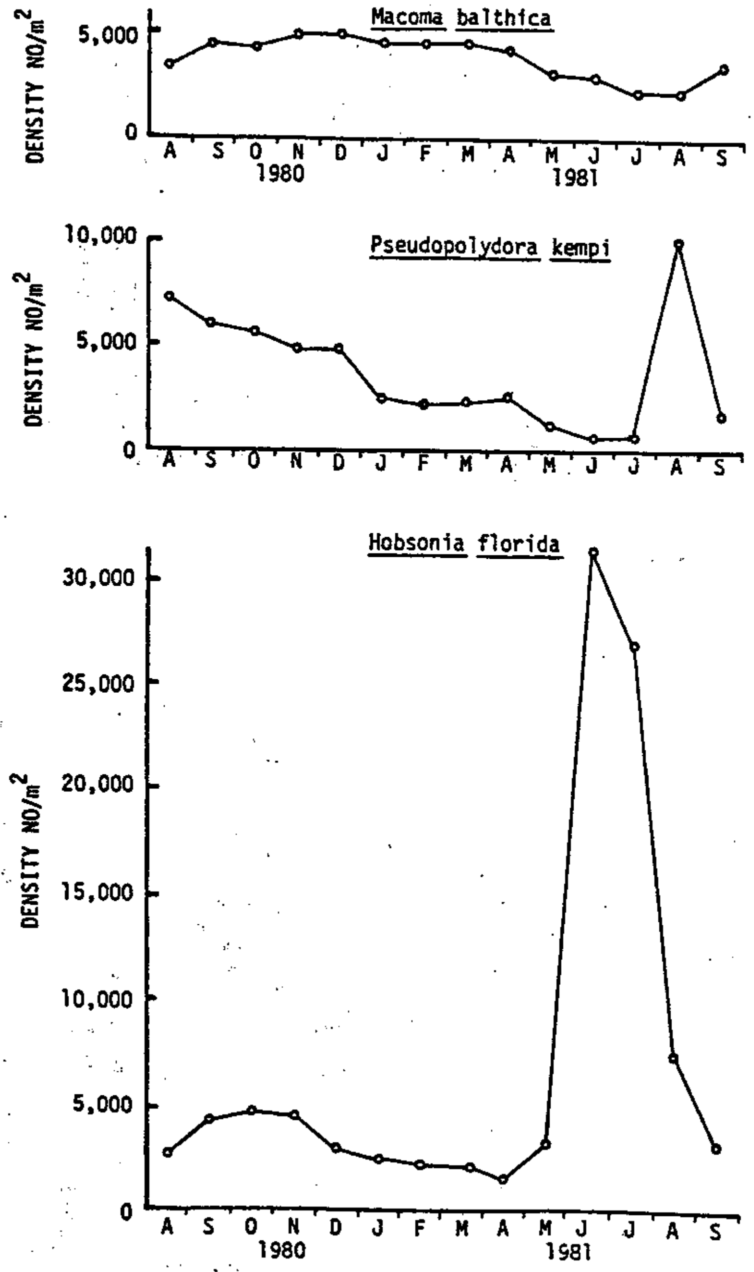


Figure 7.56 (continued).

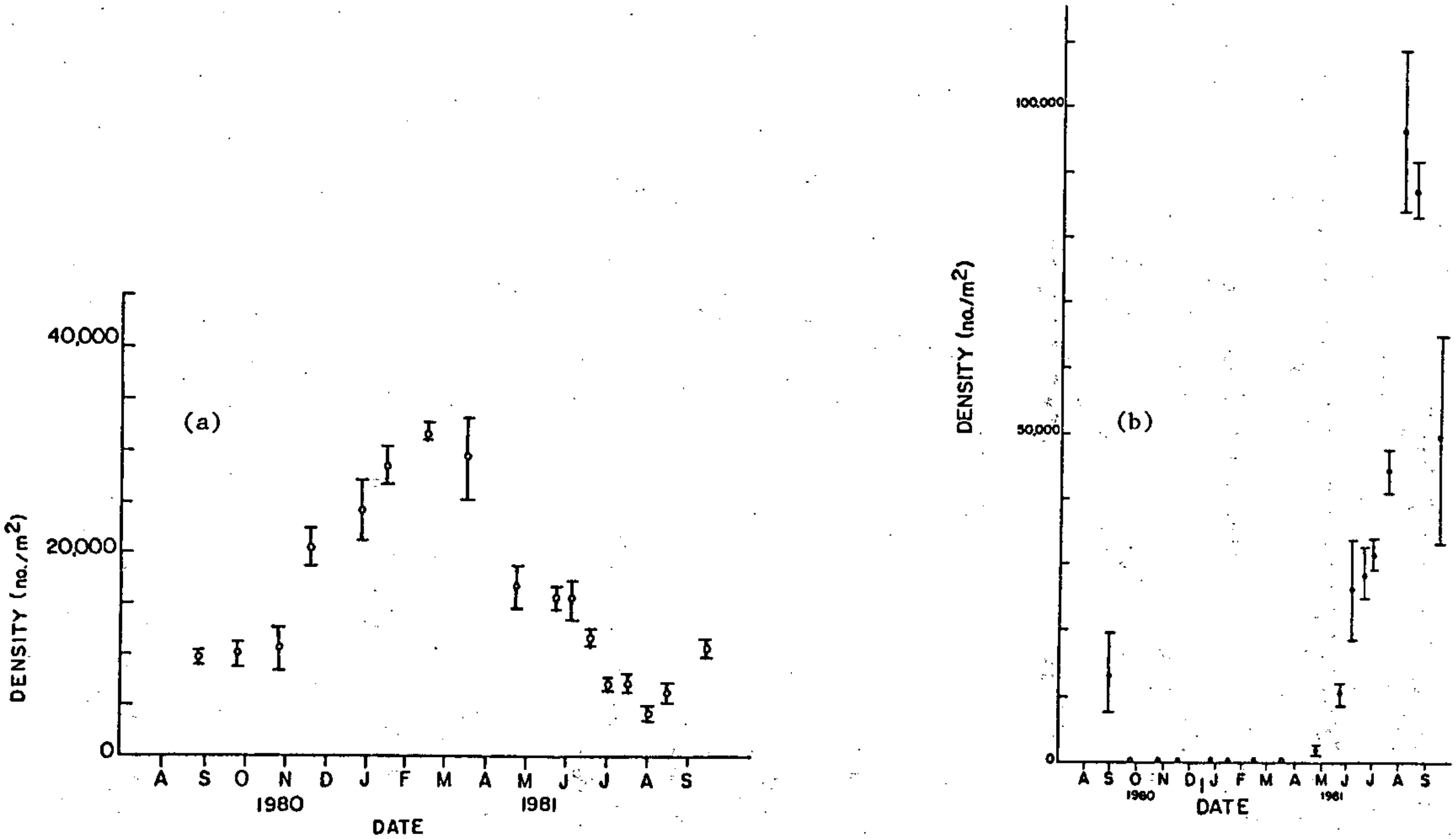


Figure 7.57. Seasonal density distributions of Corophium salmonis populations in tidal flat habitats at Desdemona Sands (a.) and Grays Bay (b.), Columbia River Estuary, September 1980 - September 1981 (Holton et al. 1984).

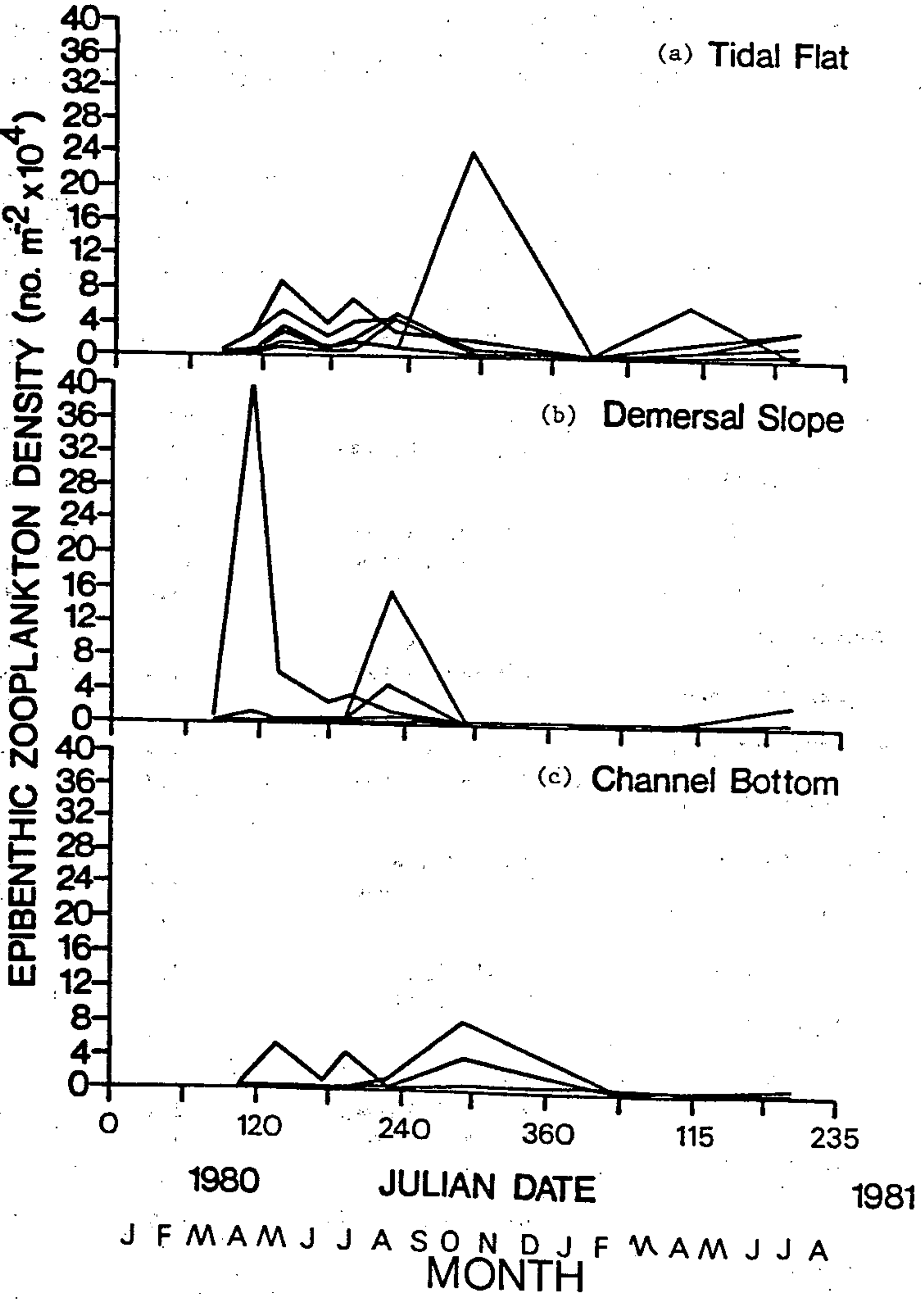


Figure 7.58. Seasonal distribution of epibenthic zooplankton density (organisms m^{-2}) in six tidal flat (a), five demersal slope (b), and five channel bottom (c) habitats in the Columbia River Estuary, March 1980 - July 1981 (Simenstad 1984).

Table 7.39. Standing crop (mgC m^{-2}) of suspension-feeding benthic infauna in different regions and habitats of the Columbia River Estuary (Data from D. Higley and R. Holton, OSU; unpubl.).

REGION	HABITAT	STANDING CROP (mgC m^{-2}) mean	±1 Standard
ENTRANCE	Tidal Flats	14.2	14.8
	Channel Bottom	44.3	63.5
Region Subtotal		38.0	57.7
BAKER-TRESTLE BAYS	Tidal Flats	77.1	45.1
	Demersal Slopes	42.6	27.9
Region Subtotal		69.6	43.8
ESTUARINE CHANNELS	Demersal Slopes	21.7	20.7
	Channel Bottom	47.2	136.4
Region Subtotal		34.4	97.4
YOUNGS BAY	Tidal Flats	25.8	17.2
	Demersal Slopes	34.0	46.5
Region Subtotal		29.4	31.2
MID-ESTUARY SHOALS	Tidal Flats	6.8	9.1
	Demersal Slopes	16.7	17.8
Region Subtotal		13.3	15.8
GRAYS BAY	Tidal Flats	0.5	0.8
	Demersal Slopes	2.5	3.4
Region Subtotal		1.5	2.6
CATHLAMET BAY	Tidal Flats	0.5	1.2
	Demersal Slopes	3.6	8.0
Region Subtotal		1.4	4.4
FLUVIAL REGION	Tidal Flats	3.4	7.9
	Demersal Slopes	2.4	3.1
	Channel Bottom	8.4	17.6
Region Subtotal		5.6	13.1
	TOTAL ALL REGIONS	24.9	59.2

Astoria-Megler Bridge. Only one channel bottom site (also near the Astoria-Megler Bridge) showed a spring-early summer density maximum, while the other four sites all illustrated peak densities in October during the low flow period (Figure 7.58c).

Due to the relatively uniform size-biomass distributions of epibenthic zooplankton, standing crop mirrored density. Average standing crop at all sites over the sampling period was 185.8+/-34.2 mg m^{-2}, ranged between 1.8 and 3,864.5 mg m^{-2}, and had a 95% confidence interval around the mean of 118.1 to 253.5 mg m^{-2}; the median was 74.0 mg m^{-2}. Regional, habitat, and temporal trends in standing stock followed those illustrated by the density data.

A more detailed itemization and discussion of regional and habitat variation in deposit-feeding epibenthic zooplankton is included in Chapter 8.

Suspension Feeding

Benthic Infauna

The magnitude of the standing stocks as well as the distributions of the two prominent suspension-feeding bivalves in the estuary, *Corbicula manilensis* and *Mya arenaria*, are quite different. *Corbicula* occur exclusively within the tidal-fluvial zone but at high levels of standing stock in all fluvial habitats--10 to 100 mgC m^{-2} in protected and unprotected tidal flats, demersal slopes, and marsh and main channels, and 1,000 to 10,000 mgC m^{-2} in minor (subsidiary) channels (Holton et al. 1984). *Mya*, on the other hand, occurs just in tidal flat and minor channel habitats in the plume and ocean zone and downriver regions of the estuarine mixing zones, and at comparatively lower standing crop levels--0.1 to 1 mgC m^{-2}. The estuary may even constitute a limiting environment for *Mya*. Holton et al. (1984) noted that they occurred at the Baker Bay intensive study site only as juveniles. The only other suspension-feeding infaunal taxon documented during the Baker Bay study, the polychaete *Polydora ligni*, may also maintain marginal populations in the estuary, as their densities peaked at between 900 and 1,000 m^{-2} during October and November 1980 but completely disappeared by June 1981. *Polydora* standing crop during the September 1981 distributional study, however, was reported as between 0.1 and 10 mgC m^{-2} in plume and ocean zone and lower estuarine mixing zone habitats except marsh channels (Holton et al. 1984).

Concentration of suspension-feeding infauna standing stock in the downriver areas of the estuary is apparent in the overall standing crop summary from the distributional survey data (Table 7.39). Maximum standing crop of suspension-feeding taxa (77.1 +/- 45.1 mgC m^{-2}) occurred in the tidal flat habitats of Baker and Trestle Bay regions and standing stocks between 30 and 50 mgC m^{-2} occurred in demersal slope and channel bottom habitats in the Entrance, Baker-Trestle Bays, Estuarine Channels, and Youngs Bay regions. Minimum standing crop (less than 5 mgC m^{-2}) occurred in all habitats of Grays and Cathlamet Bays.

Epibenthic Zooplankton

Epibenthic zooplankton densities and standing crops were described in general under Deposit Feeding. On the average, approximately half of these standing stock measures can be attributed to suspension-feeding taxa depending upon habitat and region of the estuary and hydrologic season (see Taxonomic Structure and Organization). Standing crop of the suspension-feeding component of these assemblages is further partitioned by estuarine region and habitat in Chapter 8.

Pelagic Zooplankton

Vertically-integrated standing stock of the three basic assemblages of suspension-feeding pelagic zooplankton differed both spatially along the navigational channel and temporally over the 18-month sampling period (Table 7.40, Figures 7.59-7.62). Mean densities (organisms m^{-2}) over the estuary during the 13 sampling dates (Table 7.40a) indicated that, discounting a potentially anomalous estimate (6.91 m^{-2}) from mid-July, concentrations of plume and ocean zone zooplankters remained relatively constant (about 140-240 m^{-2}) from late April until late September, and probably fluctuated below about 50 m^{-2} through autumn and winter. Many taxa were locally abundant (between 1,000 and 10,000 m^{-2}) during several periods, particularly in the low flow season when intrusion of plume and ocean water masses was at a maximum (Figure 7.59). Spatial distributions of the suspension-feeding pelagic zooplankton across the estuary generally reflected their exogenous or endogenous origins as well as potential influences of circulation dynamics of the turbidity maximum zone (Table 7.40b). Seasonally-averaged mean densities of plume and ocean zone taxa declined steadily from about 800 m^{-2} near the entrance (sampling station #1) to 0 m^{-2} near Harrington Point (sampling station #10). The density gradient was relatively constant (40-54% between stations) between Clatsop Spit (#1) and the Astoria-Megler Bridge (#5), increased (69%) in the Astoria area (#6), remained low between Astoria and Tongue Point (#7), and then again declined rapidly (74-100%) between Tongue Point and Harrington Point. Thus, relative to their import into the estuary and residence in deeper water masses, densities of these suspension feeders is more likely influenced by coastal oceanographic processes and dynamics of the zooplankton populations outside the estuary than by physical processes within.

Endemic suspension-feeding pelagic zooplankton within the estuarine mixing zone (composed principally of <u>Eurytemora affinis</u>), on the other hand, showed major density fluctuations, with the highest density estimates estuary-wide (about 1200-8200 m^{-2}) occurring during the fluctuating and high flow seasons between stations #4 and #6 (Table 7.40a). The endemic populations characteristic of the estuarine mixing zone illustrated seasonally-averaged density maxima (about 4,400 m^{-2}) between the Skipanon and Astoria sampling sites (#4 and #5, respectively) (Table 7.40b). Densities showed minor, inconsistent variation from Harrington Point to Astoria (#6) but declined steadily (28-45% between stations) between that point and the entrance. Local densities were at their maximum in the estuarine mixing zone during April and May but relatively high (10,000-100,000 m^{-2}) densities

Table 7.40. Mean densities (no. m^{-2}) of three assemblages of suspension-feeding pelagic zooplankton by date (a) and station (b) during CREDDP sampling in the Columbia River Estuary, April 1980-April 1981.

a. ZOOPLANKTON ASSEMBLAGES	SAMPLING DATE 1980												1981
	4/29	5/13	5/28	6/10	6/25	7/15	8/5	8/19	9/3	9/16	9/30	12/6	4/29
Plume & Ocean	141.48	239.72	213.07	233.78	231.9	6.91	222.14	177.96	194.04	186.45	39.75	22.94	372.2
Estuarine Mixing	8197.36	3351.92	2708.33	1186.29	1929.78	2317.56	554.84	208.43	1148.21	545.76	208.25	77.01	920.75
Tidal-Fluvial	265.07	229.37	174.21	91.98	147.76	180.34	289.30	108.16	287.46	69.65	56.65	16.99	128.13

b. ZOOPLANKTON ASSEMBLAGES	SAMPLING STATION 1	2	3	4	5	6	7	8	9	10
Plume & Ocean	812.96	443.94	264.82	121.16	55.26	16.87	17.65	4.62	0.88	0.00
Estuarine Mixing	1307.23	1197.11	1062.01	4365.61	4449.19	2984.81	597.20	590.64	615.16	268.76
Tidal-Fluvial	27.85	38.46	62.42	113.12	168.05	256.73	229.55	228.85	233.09	279.68

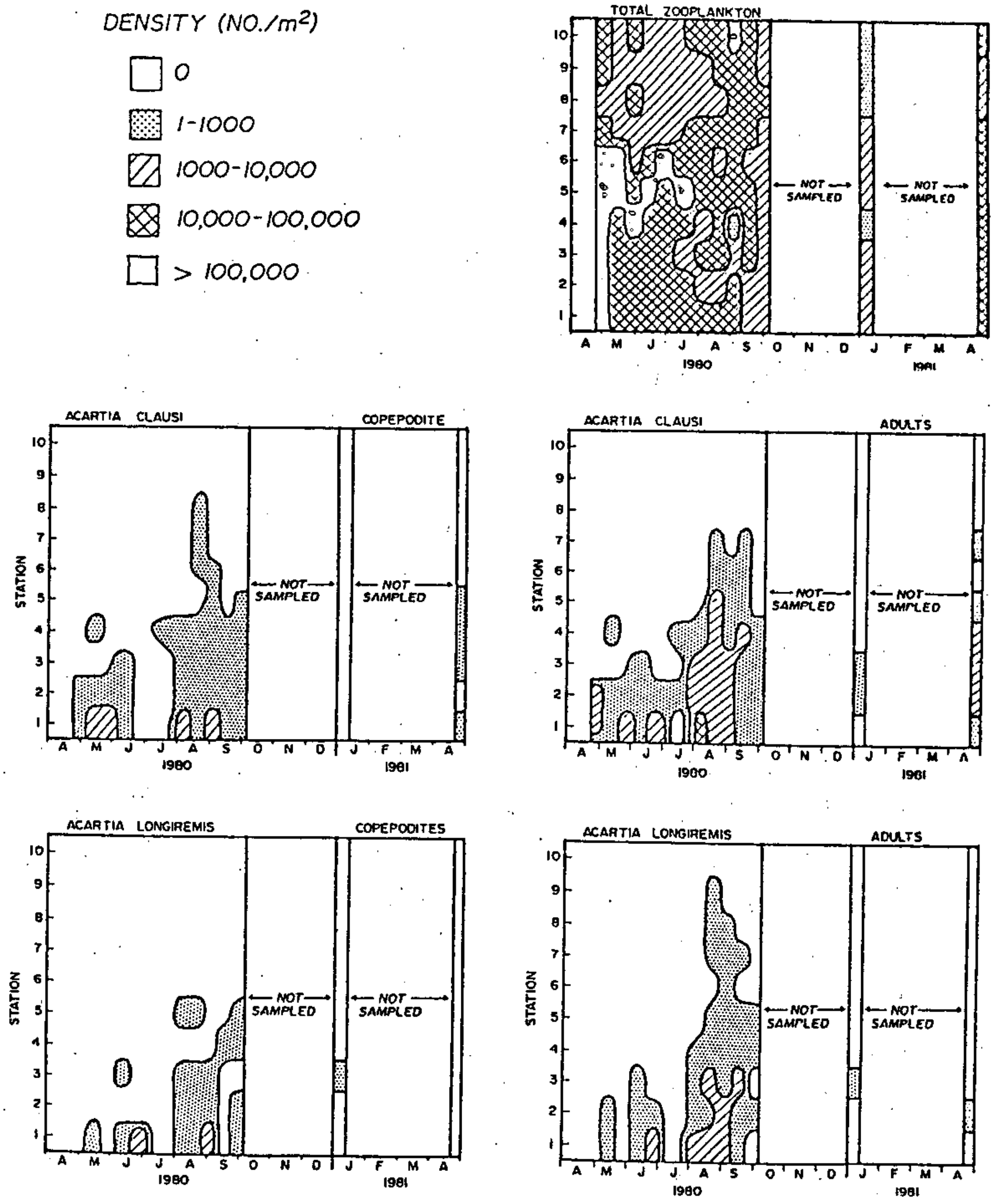


Figure 7.59. Seasonal density of total zooplankton and lower estuary copepods.

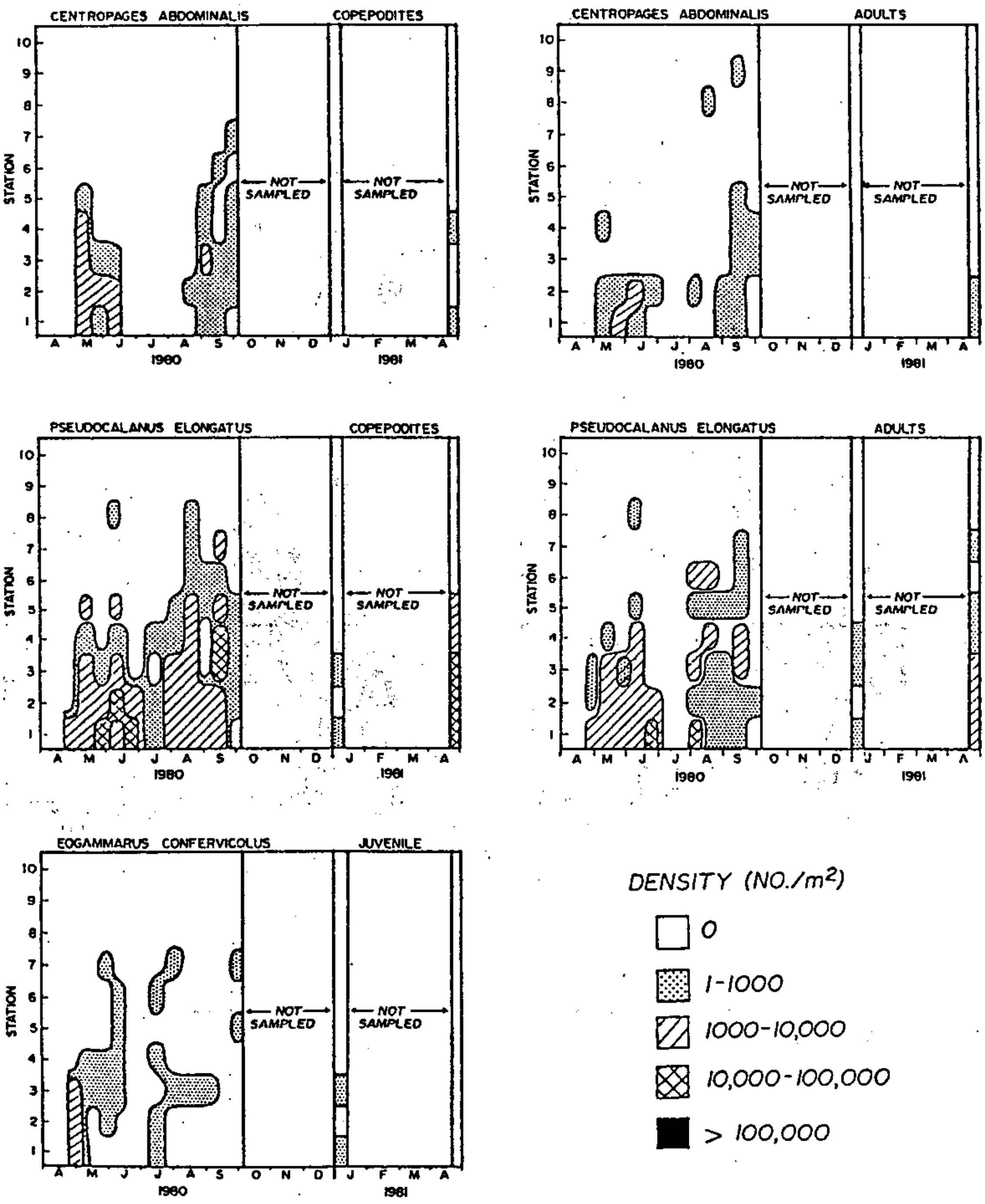


Figure 7.59 (continued). Seasonal density of lower estuary copepods and amphipods.

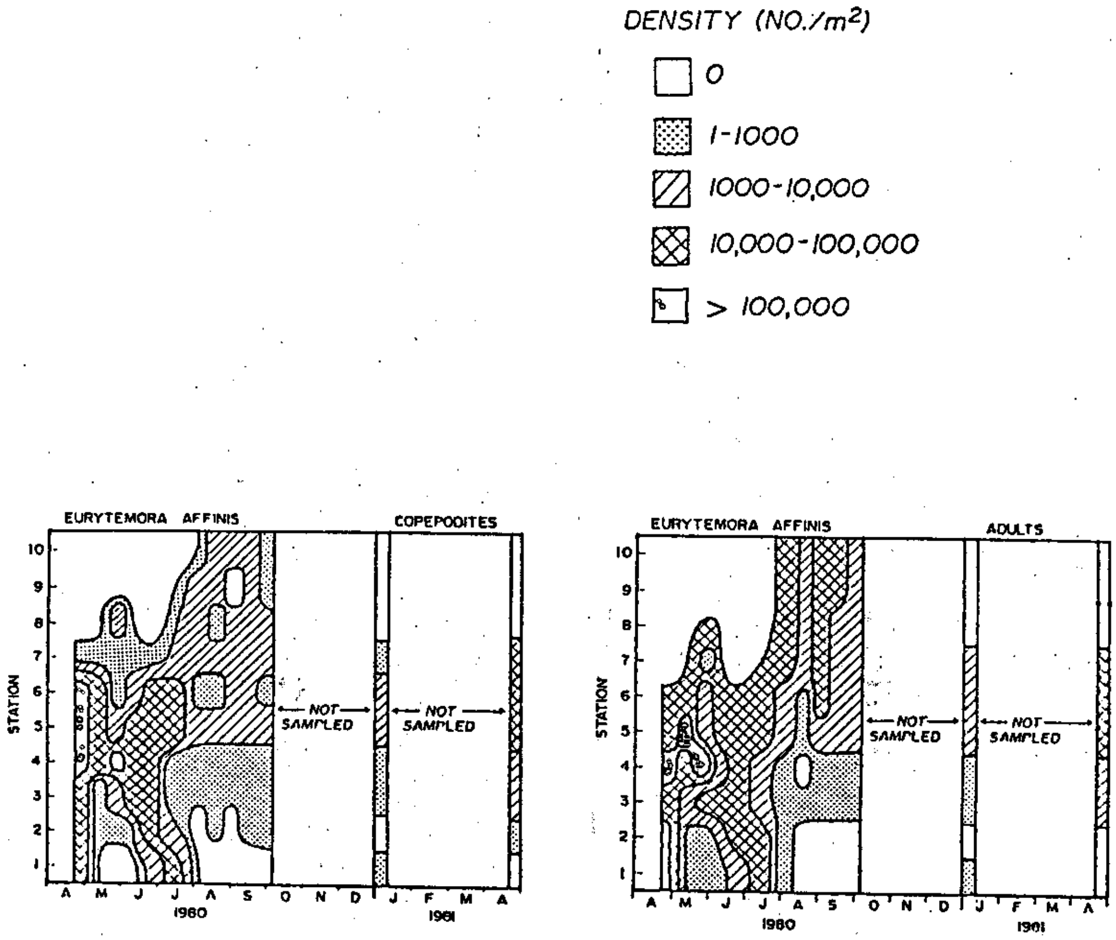


Figure 7.60. Seasonal density of estuarine mixing zone pelagic zooplankton (Jones and Bottom 1984).

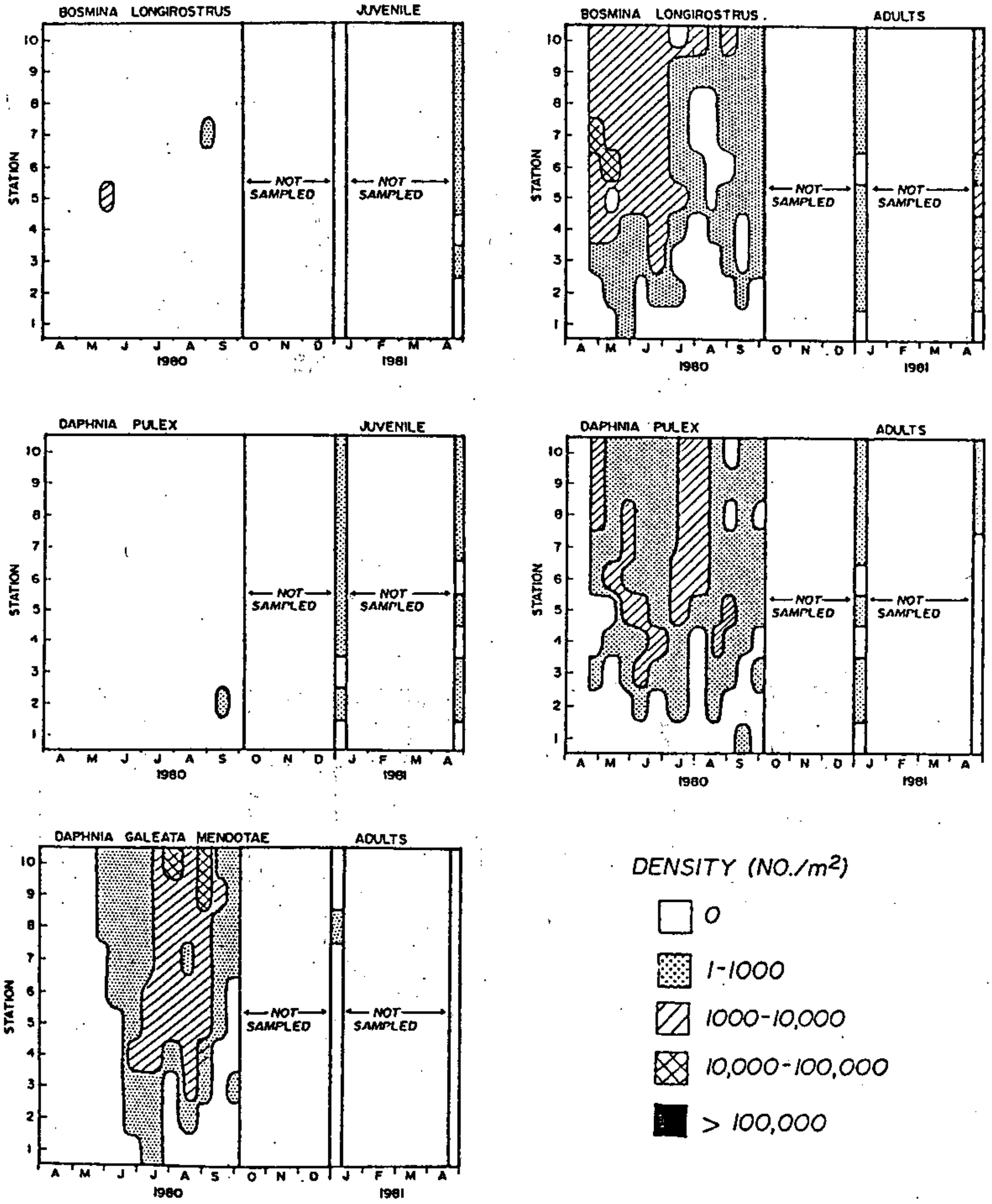


Figure 7.61. Seasonal density of tidal-fluvial pelagic zooplankton (Jones and Bottom 1984).

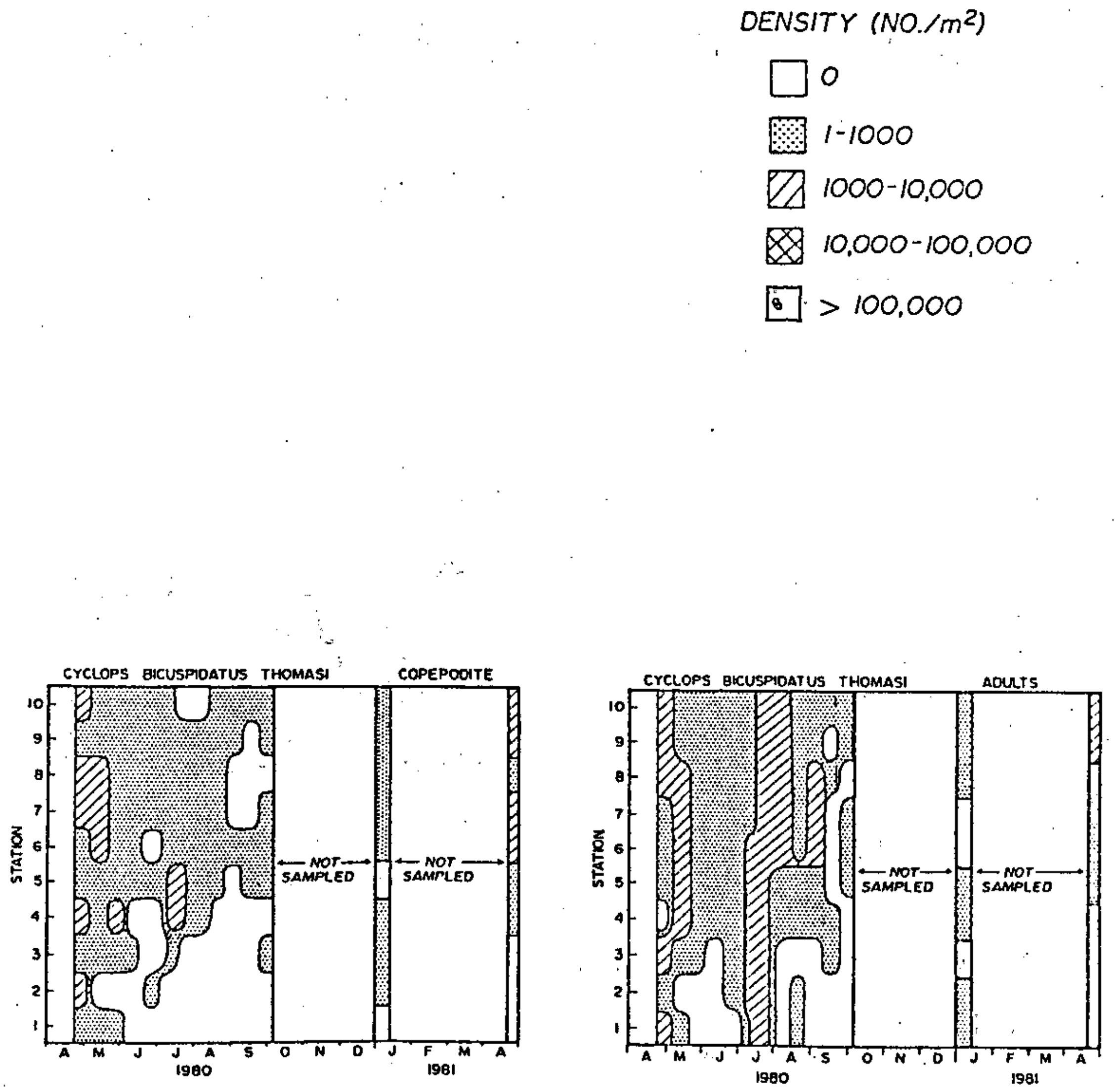


Figure 7.61 (continued).

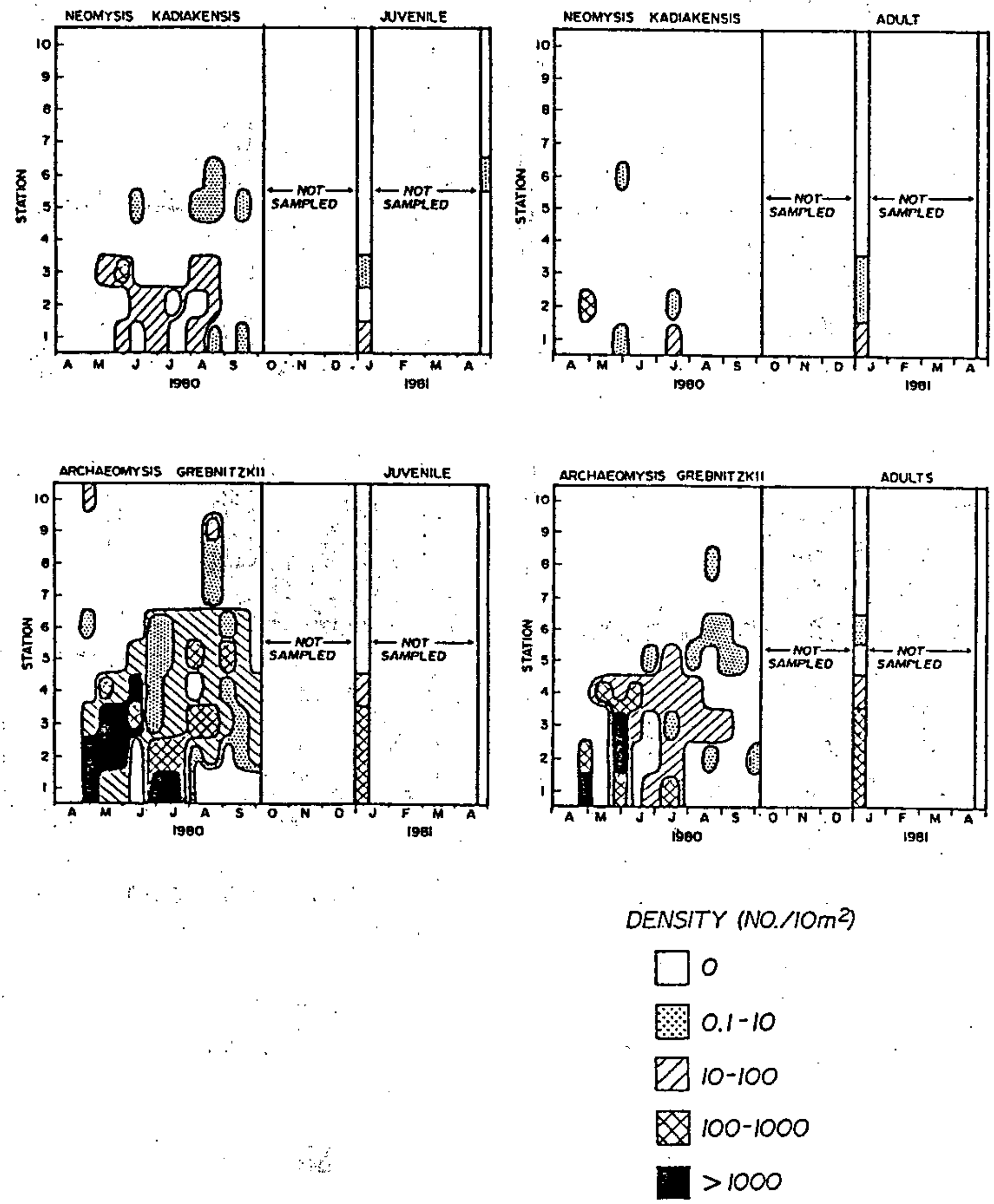


Figure 7.62. Seasonal density of lower estuary mysids.

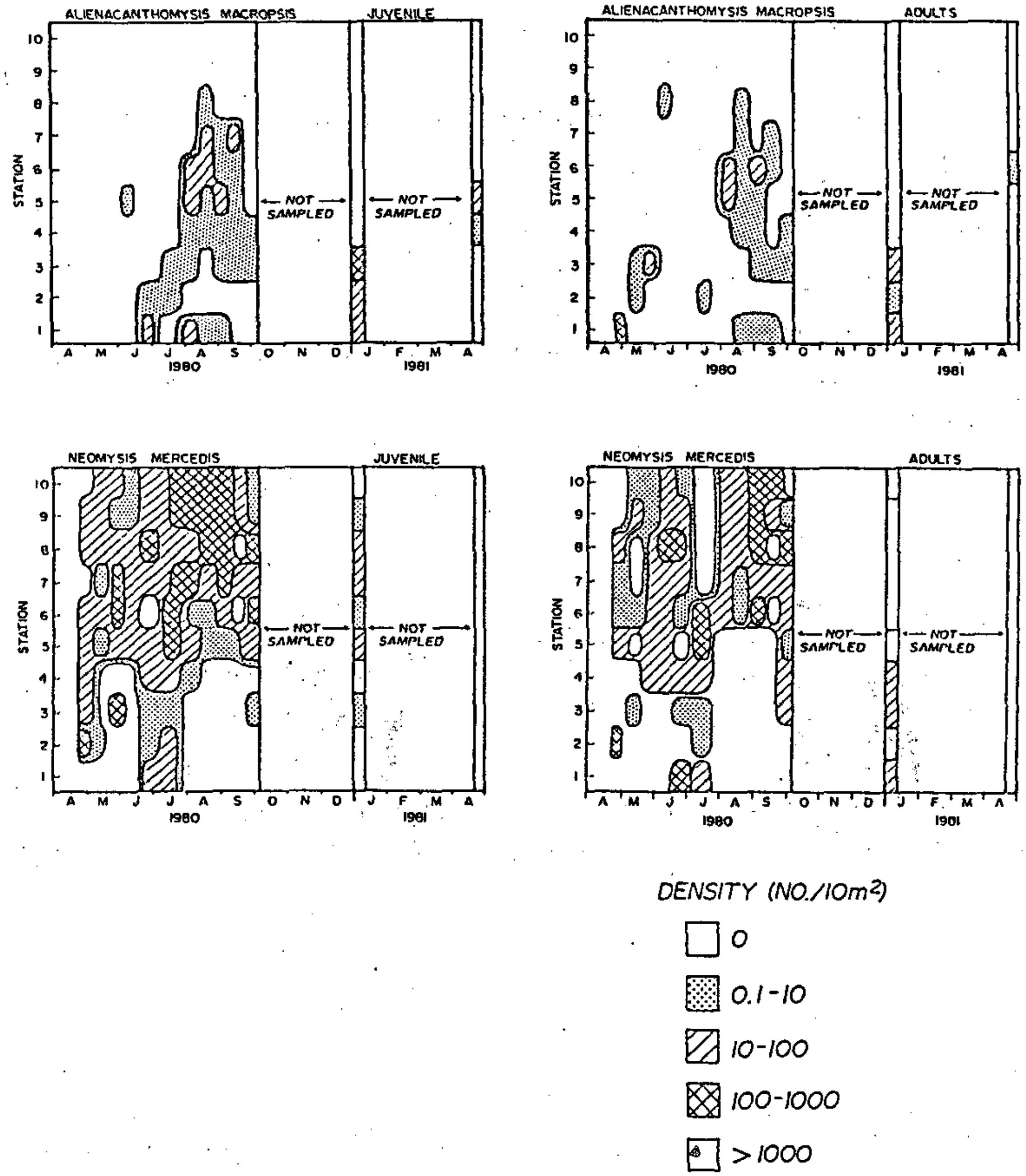


Figure 7.62 (continued). Seasonal density of mid- and upper estuary mysids.

occurred throughout the estuary through the low flow season as salinity intrusion increased (Figure 7.60). These density patterns in estuarine mixing zone pelagic zooplankton indicate that the zone's circulation processes, particularly salinity intrusion and the position of the turbidity maximum zone, are probably the principal influences upon local density structure, while dynamics of the endemic population determine the temporal variation.

Pelagic zooplankton originating from the tidal-fluvial zone (and upriver from the estuary) varied over a comparatively narrow density range (about 17-289 m^{-2} estuary-wide) throughout the sampling period (Table 7.40). Local density maxima (10,000-100,000 m^{-2}) varied by taxa, however (Figure 7.61). For example, peak densities of adult Bosmina longirostris occurred during the high flow season while Daphnia galeata mendotae tended to be more dense during the low flow season. As might be expected, seasonally-averaged densities increased with position upriver, from less than 100 m^{-2} below the Skipanon River to more than 200 m^{-2} above Astoria. Thus, given the comparably constant import of fluvial water into the estuary, densities of these freshwater zooplankters are probably more a function of upriver population dynamics than of estuarine circulation. Local densities, however, may be affected by mixing and other circulation processes.

Predation

Benthic Infauna

Highest standing stock levels of the predatory polychaetes Eteone spp. and Nephtys californiensis were reported in the tidal-fluvial zone during the September 1981 distributional survey (Holton et al. 1984). The phyllodocid Eteone spp. were most dense, 10 to 100 mgC m^{-2}, in protected tidal flats; they occurred at intermediate standing crop levels, 1 to 10 mgC m^{-2} in unprotected tidal flat, demersal slope, and marsh channel habitats; lowest standing crops, 0.1 to 1 mgC m^{-2}, occurred in minor channels. Although the distribution of Eteone also extended into the estuarine mixing zone, their standing crop was relatively depressed, 0.1 to 1 mgC m^{-2} in demersal slope habitats and 0.01 to 0.1 mgC m^{-2} in tidal flat habitats. Nephtys occurred exclusively in higher energy tidal-fluvial zone habitats at standing crop levels of 1 to 10 mgC m^{-2}. Eteone spp. at the Baker Bay intensive study site were present throughout the year at densities below 100 m^{-2} but declined to below 10 m^{-2} during the high flow season (Holton et al. 1984).

The gammarid amphipod Eogammarus confervicolus, classified as a predator by Holton et al. (1984), was extremely common throughout the estuary, particularly so in the estuarine mixing and tidal-fluvial zones, where standing crop generally varied between 0.1 and 10 mgC m^{-2} (Holton et al. 1984). Eogammarus was neither common nor abundant enough at the Baker Bay study site to report seasonal trends (Holton et al. 1984).

The predominance of predatory infauna taxa in the upriver areas of the estuary is also illustrated in the summary of standing crop values from the distributional survey data (Table 7.41). The fluvially-influenced Cathlamet Bay and Fluvial Regions had mean standing crop levels between about 375 and 500 mgC m^{-2}, with standing crop maxima occurring in channel bottom (800 mgC m^{-2}) and demersal slope (about 235-292 mgC m^{-2}) habitats. In marked contrast, standing crop values in all other regions were less than 100 mgC m^{-2} and the Entrance and Youngs Bay Regions had no measurable populations at all.

Motile Macroinvertebrates

Motile macroinvertebrate density averaged 0.09 +/- 0.02 m^{-2} across the estuary, ranging between 0 and 1.72 m^{-2} with a 95% confidence interval of 0.04 and 0.14 m^{-2}. As with the epibenthic zooplankton, motile macroinvertebrate densities were higher in tidal flat habitats (0.12+/-0.04 m^{-2}) than in demersal slope (0.08+/-0.04 m^{-2}) or channel bottom habitats (0.07+/-0.04 m^{-2}). Standing crop of Dungeness crab and crangonid shrimp, the dominant motile macroinvertebrates, averaged 0.17+/-0.06 g^{-2}, ranged between 0 and 6.34 g m^{-2}, with a 95% confidence interval around the mean of 0.05 to 0.30 g m^{-2}.

Density and standing crop distributions through the estuary changed dramatically among hydrologic seasons. These standing stock shifts were specifically associated with movements of Crangon franciscorum and Neomysis mercedis as Cancer magister was almost always confined within the Entrance Region. Macroinvertebrate density in tidal flat habitats during the high flow season were highest within 20 km of the estuary's mouth (about 0.1 to 0.3 m^{-2}) but had expanded, though in lower density (about 0.1 m^{-2}), to Grays Bay (km 32) during the low flow season. By the fluctuating flow season densities had both decreased below 0.1 m^{-2} throughout the estuary as well as become concentrated back in the peripheral bays in the downriver regions of the estuary. Densities of motile macroinvertebrates in demersal slope habitats were considerably denser (as high as 1 m^{-2}) in the central regions of the estuary (Desdemona Sands) during the high flow season and showed the same low flow season expansion to the lower reaches of the tidal-fluvial zone. Although densities in channel bottom habitats during the high flow season were lower (less than 0.2 m^{-2}) than in the shallower habitats, the highest density during low flow months (about 1 m^{-2}) occurred in the channel near Rice Island. By the fluctuating flow season densities had again declined in channels throughout the estuary. Trends in seasonal distributions of standing crop resembled those of density, although sites in the plume and ocean zone during high and fluctuating flow seasons and lower reaches of the estuarine mixing zone during low flow months showed slightly higher standing crop levels than the other sites due to the presence of the larger Dungeness crab.

Pelagic Zooplankton and Larval Fish

In contrast to suspension-feeding pelagic zooplankton, predatory zooplankton and larval fish assemblages showed similar density distributions over time and space (Table 7.42). Larval fish and only a few taxa of pelagic zooplankton (e.g., Sagitta elegans) were characteristic of plume and ocean zone assemblage predators. In contrast, pelagic zooplankters (almost exclusively mysids) dominated the

Table 7.41. Standing crop (mgC m^{-2}) of predatory benthic infauna in different regions and habitats of the Columbia River Estuary (Data from D. Higley and R. Holton, OSU; unpubl. data).

REGION	HABITAT	STANDING CROP (mgC m^{-2}) mean	STANDING CROP (mgC m^{-2}) ±1 Standard
ENTRANCE	Tidal Flats	0	0
	Channel Bottom	0	0
Region Subtotal		0	0
BAKER-TRESTLE BAYS	Tidal Flats	4.5	19.1
	Demersal Slopes	2.5	4.0
Region Subtotal		4.1	16.9
ESTUARINE CHANNELS	Demersal Slopes	24.9	110.2
	Channel Bottom	5.9	15.9
Region Subtotal		15.4	78.5
YOUNGS BAY	Tidal Flats	0	0
	Demersal Slopes	0	0
Region Subtotal		0	0
MID-ESTUARY SHOALS	Tidal Flats	3.8	10.7
	Demersal Slopes	7.8	16.9
Region Subtotal		6.4	14.9
GRAYS BAY	Tidal Flats	26.2	20.9
	Demersal Slopes	22.4	26.2
Region Subtotal		24.3	22.7
CATHLAMET BAY	Tidal Flats	292.3	997.9
	Demersal Slopes	573.4	970.9
Region Subtotal		372.6	980.8
FLUVIAL REGION	Tidal Flats	144.1	90.2
	Demersal Slopes	235.5	412.4
	Channel Bottom	799.6	1,513.2
Region Subtotal		499.3	1,117.2
	TOTAL ALL REGIONS	137.7	603.1

Table 7.42. Mean densities (no. m^{-2}) of three assemblages of predatory pelagic zooplankton and larval fish by date (a) and station (b) during CREDDP sampling in the Columbia River Estuary, April 1980-April 1981.

a.	SAMPLING DATE												
	1980												1981
ASSEMBLAGES	4/29	5/13	5/28	6/10	6/25	7/15	8/5	8/19	9/3	9/16	9/30	12/6	4/29
Plume & Ocean	0.41	63.30	2.12	1.37	0.07	0.05	0.26	0.08	1.14	1.06	0.91	2.84	19.56
Estuarine Mixing	117.60	6.29	13.37	2.38	1.80	4.08	0.90	0.80	1.97	0.21	0.50	2.18	3.26
Tidal-Fluvial													

b.	SAMPLING STATION									
ASSEMBLAGES	1	2	3	4	5	6	7	8	9	10
Plume & Ocean	26.00	23.21	15.64	6.33	0.39	0.02	0.02	0.01	0	0
Estuarine Mixing	61.23	27.34	9.04	3.78	2.55	3.28	2.78	3.00	3.00	3.37
Tidal-Fluvial										

planktonic predators in the estuarine mixing zone assemblage while larval fish (e.g., Cottus asper) were not prominent components. Temporal and spatial distributions of mysid densities varied by taxa (Figure 7.61). The predominantly plume and ocean zone mysids (Neomysis kadiakensis, Archaeomysis grebnitzkii) illustrated density maxima at stations below Astoria (100-1,000 m^{-2}) primarily during the high and early low flow seasons. The endemic mysids (Neomysis mercedis, Alienacanthomysis macropsis) in the estuarine mixing zone showed more variable densities, with maxima (also 100-1,000 m^{-2} for N. mercedis) at several periods and locations throughout the sampling period and estuary. Density maxima did tend to move upriver between the high flow season and the low flow season. There were neither vertebrate nor invertebrate planktonic predators identified from the tidal-fluvial zone assemblages.

Larval fish from the plume and ocean zone were densest (19.6-63.3 m^{-2}) during the months of April and May but densities declined rapidly to less than 1 m^{-2} between June and August (Figure 7.63). Estuarine mixing zone assemblages indicated a similar pattern of density maxima (6.3-117.6 m^{-2}) during April and May. Both assemblages also showed steadily decreasing density gradients from the mouth toward the head of the estuary. Plume and ocean zone assemblage density was highest (26 m^{-2}) at Clatsop Spit and declined steadily up the estuary, with the sharpest decline (60-94%) between the sampling stations off Fort Stevens (#3) and the Astoria-Megler Bridge (#5). Estuarine mixing zone assemblage density was also concentrated in the lower area of the estuary. Maximum density (about 61 m^{-2}) occurred at Clatsop Spit and declined rapidly (55-67%) between there and Youngs Bay but remained quite constant from that point on up the estuary. Except for Cottus asper, the density data was too variable to indicate temporal-spatial trends. The endemic C. asper occurred in maximum local densities (100-1,000 m^{-2}) in the estuarine mixing zone during early high flow months and declined dramatically, apparently metamorphosing to demersal juveniles prior to the low flow season. Other fish larvae were only sporadically dense, primarily during the initial segment of the sampling period.

Fish

Fish density and standing crop were estimated from total catch number and biomass data (McConnell et al. 1983) by assuming standardized areal effort (m^{-2}) for each of the three quantitative sampling methods used during the finfish investigations in the estuary. In addition, coincident fish density and standing crop data obtained during the epibenthic zooplankton and motile macroinvertebrate sampling was incorporated into the dataset for tidal flat habitats, which were not surveyed in the finfish investigations (Bottom et al. 1984).

Seasonally-averaged density (fish m^{-2}) and standing crop (g m^{-2}) are summarized (range, mean +/- one standard deviation) in Table 7.43. Water column fishes (i.e., pelagic, schooling fishes and some epibenthic forms) occurred in densities as high as 0.28 m^{-2} and standing crops as high as 3.56 g m^{-2}, with the highest standing stock occurring in the Entrance Region (average density, 0.07+/-0.10 m^{-2}; average standing

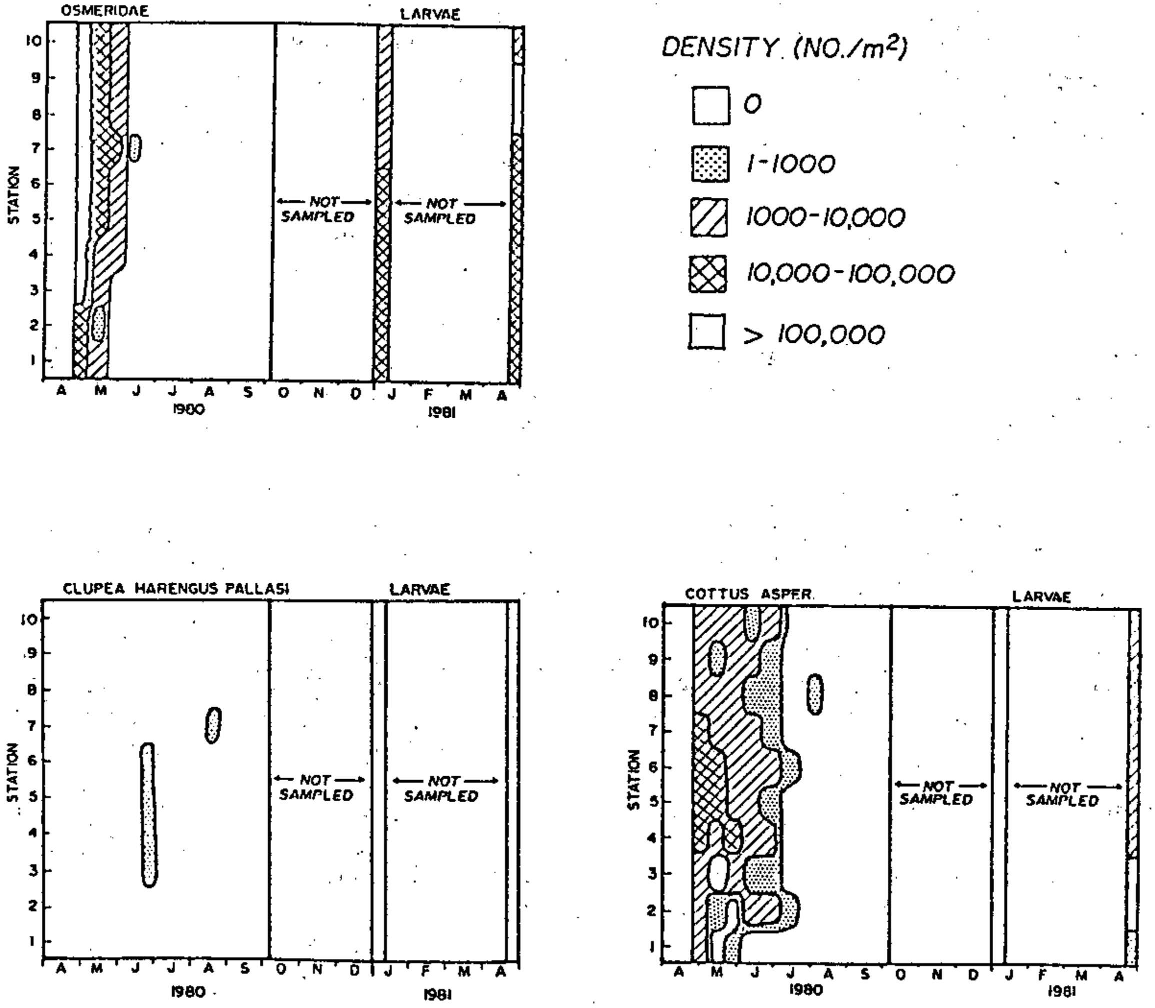


Figure 7.63. Seasonal density of fish eggs and larvae in the Columbia River Estuary.

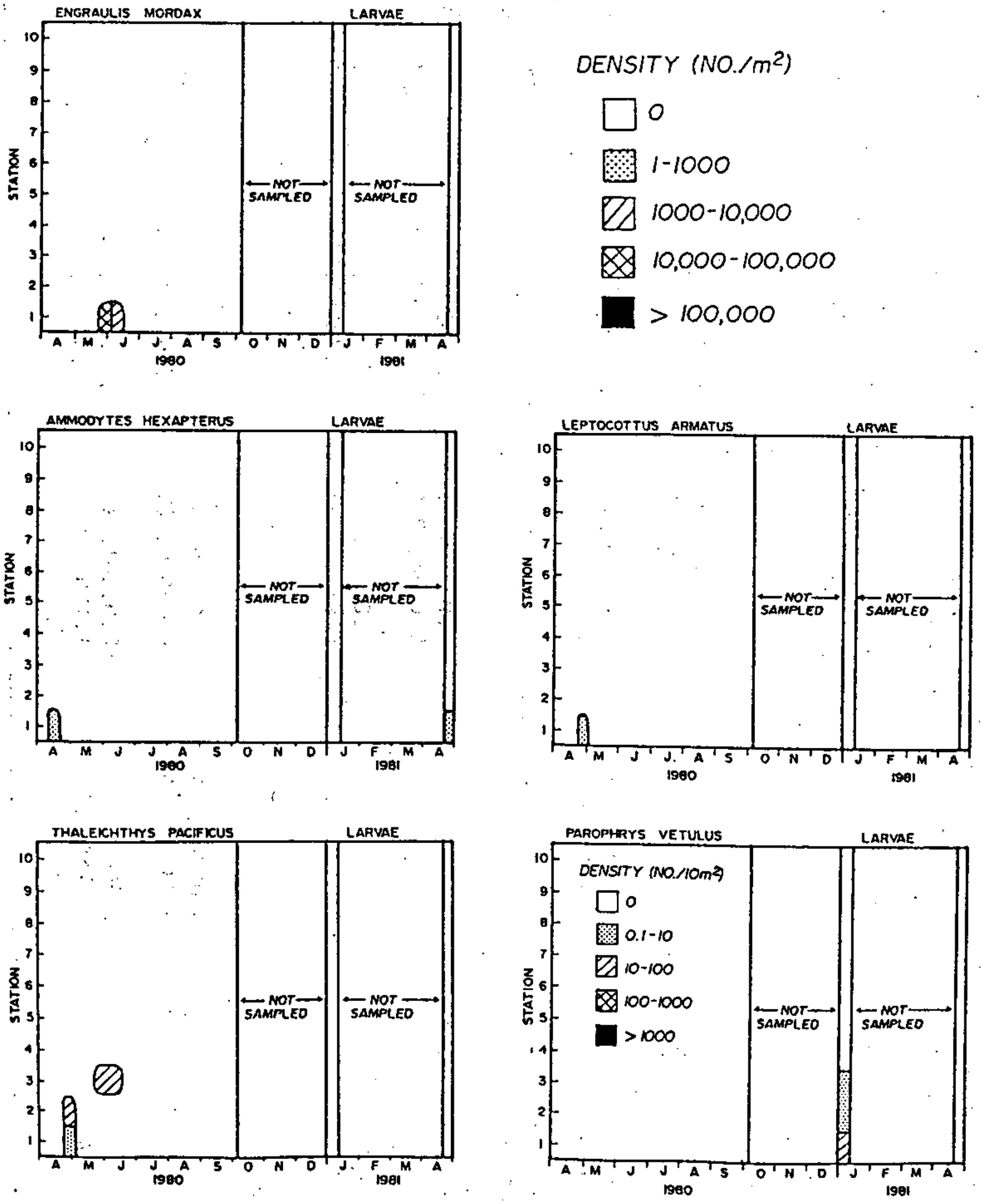


Figure 7.63 (continued). Seasonal density of fish eggs and larvae in the lower Columbia River Estuary.

Table 7.43. Range (minimum-maximum) and mean (± 1 standard deviation) of fish density (no. m^{-2}) and standing crop (g m^{-2}) in four habitats and eight regions of Columbia River Estuary between March 1980 and September 1981. (McConnell et al. 1983, and Simenstad, UW, unpubl.)

HABITATS Sampling Area	Water Column ($7959m^2$)	Demersal Slope ($2713m^2$)	Channel Bottom ($2944m^2$)	Tideflat ($750m^2$)
ENTRANCE				
Density; min-max	0.001-0.275	0.001-0.034	0.011-0.098	
mean	0.065±0.100	0.018±0.018	0.037±0.035	
Standing crop; min-max	0.018-3.556	0.019-0.212	0.141-3.885	
mean	1.181±1.494	0.156-0.092	1.302±1.134	
BAKER BAY & TRESTLE BAY				
Density; min-max		0.001-0.127	0.065-0.200	<0.01-0.32
mean		0.036±0.044	0.141±0.064	0.068±0.103
Standing crop; min-max		0.012-1.138	1.714-3.619	<0.100-4.80
mean		0.476±0.437	2.722±0.818	1.020±1.545
ESTUARINE CHANNELS				
Density; min-max	0.003-0.197	0.006-0.104	0.002-1.001	
mean	0.031±0.036	0.046±0.043	0.071-0.150	
Standing crop; min-max	0.066-2.900	0.062-2.531	0.077-11.656	
mean	0.478±0.553	1.130±1.026	1.510±1.951	

Table 7.43. (Continued).

HABITATS Sampling Area	Water Column (7959m^2)	Demersal Slope (2713m^2)	Channel Bottom (2944m^2)	Tideflat (750m^2)
YOUNGS BAY				
Density; min-max		0.010-0.279	0.068-0.151	0.01-0.56
mean		0.084±0.097	0.102±0.036	0.102±0.168
Standing crop; min-max		0.216-3.131	1.216-2.025	0.150-8.400
mean		0.983±0.978	1.690±0.369	1.530±2.529
MID-ESTUARY SHOALS				
Density; min-max		0.001-0.070		0.010-2.30
mean		0.024±0.024		0.294±0.753
Standing crop; min-max		0.015-1.050		0.150-34.50
mean		0.360±0.360		4.410±11.295
GRAYS BAY				
Density; min-max	0.015-0.083	0.004-0.095	0.041-0.104	0.01-0.17
mean	0.051±0.028	0.036±0.043	0.076±0.031	0.056±0.056
Standing crop; min-max	0.237-1.062	0.026-1.523	0.347-2.356	0.150-2.55
mean	0.573±0.384	0.623±0.655	1.188±0.882	0.842±0.842
CATHLAMET BAY				
Density; min-max	0.005-0.030	0.017-0.114	0.003-0.026	
mean	0.017±0.011	0.059±0.050	0.014±0.009	
Standing crop; min-max	0.104-1.176	0.818-4.306	0.099-0.725	
mean	0.600±0.467	2.443±1.451	0.312±0.212	

Table 7.43. (Continued).

HABITATS Sampling Area	Water Column (7959m^2)	Demersal Slope (2713m^2)	Channel Bottom (2944m^2)	Tideflat (750m^2)
FLUVIAL				
Density; min-max	0.002-0.032	0.011-0.062	0.001-0.046	0.02-0.06
mean	0.010±0.009	0.036±0.017	0.012±0.014	0.036±0.018
Standing crop; min-max	0.085-0.860	0.087-1.739	0.025-1.707	0.30-0.90
mean	0.371±0.245	0.599±0.542	0.428±0.526	0.540±0.272

crop, 1.18+/-1.49 g m^{-2}). Demersal slope assemblages (principally epibenthic fishes) occurred in densities as high as 0.28 m^{-2} and standing crops as high as 4.31 g m^{-2}, with the highest average density (0.08 m^{-2}) occurring in the Youngs Bay Region and the highest average standing crop (2.44 g m^{-2}) occurring in the Cathlamet Bay Region. In comparison, channel bottom assemblages (demersal fishes) typically illustrated higher densities and standing crops, as high as 1 m^{-2} and 11.66 g m^{-2}, respectively. Although not sampled as intensively, sampling of tidal flat habitats in five regions indicated some of the highest fish standing stock of any habitat. Densities as high as 2.3 m^{-2} and standing stocks as high as 34.5 g m^{-2} were documented and the average density (0.29+/-0.75 m^{-2}) and standing crop (4.41+/-11.30 g m^{-2}) in the Mid-estuary Shoals Region constituted the highest measured in the estuary.

On a seasonal basis, the estuary's fish populations were highest during the summer, averaging twice as high as during any other season (Bottom et al. 1984).

Terrestrial and Aquatic Mammals

Merker and Fenton (1984) made whole-estuary estimates of the densities of herbivorous and predatory terrestrial and aquatic mammals based on population estimates and the area of the different habitats occupied. They found nutria to range between 2.5 an 20.8 animals ha^{-1}; muskrat, 0.75 and 6.6 ha^{-1}; American beaver, 0.28 ha^{-1}; Columbian white-tailed deer, 0.02 to 0.06 ha^{-1}; black-tailed deer, 0.08 ha^{-1}; raccoon 0.08 ha^{-1}; and Canadian river otter, 0.02 ha^{-1}. Although no standing stock estimates *per se* were generated, partitioning of the density data by life history and sex composition of the respective populations and expansion by average biomass of juvenile, female, and male animals provides approximate estimates of the standing crop of these animals: nutria, 7.63 to 62.98 kg wet weight ha^{-1}; muskrat, 0.74 to 6.48 kg wet weight ha^{-1}; American beaver, 3.16 kg wet weight ha^{-1}; Columbian white-tailed deer, 0.85 to 2.56 kg wet weight ha^{-1}; black-tailed deer, 3.42 kg wet weight ha^{-1}; raccoon, 0.32 kg wet weight ha^{-1}; and Canadian river otter, 0.17 kg wet weight ha^{-1}.

Marine Mammals

Jeffries et al. (1984) summarized the standing stock of marine mammals by season and estuarine zone (Table 7.44). Highest densities observed (4.25-4.61 km^{-2}) were for harbor seals in the estuarine mixing zone during spring and summer, which corresponded to standing crop estimates of 322.73-349.58 kg wet weight km^{-2}. Overall, total marine mammal (pinniped) densities ranged from 1.25 km^{-2} in autumn to 3.55 km^{-2} in spring, and standing crop estimates varied correspondingly between 105.53 kg wet weight km^{-2} and 332.40 kg wet weight km^{-2}. Standing crop was, however, higher during the summer (347.87 kg wet weight km^{-2}) because of the higher densities of the larger sea lions to the plume and ocean zone.

Table 7.44. Density (no.km^{-2}) and standing crop (kg wet km^{-2}) of marine mammals during CREDDP sampling in Columbia River Estuary during four seasons, 1980-1981. Data from Jeffries et al. 1984.

Season	Taxa	ESTUARINE ZONES						ESTUARY TOTAL	
		Plume & Ocean		Estuarine-Mixing		Tidal-Fluvial			
		density	standing crop	density	standing crop	density	standing crop	density	standing crop
SPRING (March-May)	Sea lions	2.62	785.56	0.06	17.68	0	0	0.29	85.76
	Harbor seals	0	0	4.25	322.73	2.61	198.18	3.25	246.64
SUMMER (June-August)	Sea lions	4.72	1422.51	0.03	6.31	0	0	0.47	141.32
	Harbor seals	0	0	4.61	349.58	0.56	42.43	2.70	206.55
AUTUMN (September-November)	Sea lions	0.50	148.62	0	0	-	-	0.05	14.41
	Harbor seals	0	0	2.21	167.76	0	0	1.20	91.12
WINTER (December-February)	Sea lions	1.11	332.63	0	0	0	0	1.36	32.24
	Harbor seals	0.02	1.79	2.38	184.37	0.19	8.68	0.11	103.45

7.3.4 Process Dynamics

Resource Inputs

Where the actual food resources were known, either on a taxon-specific (e.g., based on stomach contents, feeding site or foraging observations) or a functional group (e.g., suspension-feeding phytoplankton) basis, the magnitude and often the temporal-spatial variability of consumption rates were measured or directly estimable from CREDDP data. In some cases (e.g., deposit feeders on detritus), consumption had to be estimated from literature values for energy budgets documented from similar estuarine communities and fauna.

Wetland Herbivory

Emergent vascular plants comprise the principal (food) resource inputs to the wetland herbivores. Merker and Fenton (1984) provided estimates of the consumption rates of the estuary's muskrat, nutria, and beaver populations. Above-ground vascular plant consumption by muskrats was determined to be 506 to 4,455 MT fresh weight yr^{-1} or, assuming a 20% fresh weight-dry weight conversion, 101 to 891 MT dry wt yr^{-1}. Assuming that plant carbon is 40% of dry weight, muskrat consumption is estimated to range between 40 and 356 MT C yr^{-1}. Similar extrapolations of annual aboveground plant consumption by nutria (3,973-33,062 MT fresh weight yr^{-1}) and beaver (176-200 MT yr^{-1}) indicate that they extract 318 to 2,645 MT C yr^{-1} and 14 to 16 MT C yr^{-1}, respectively, in emergent vascular plant carbon from swamp and low and high marsh habitats in the estuary. Thus, the three principal wetland herbivores account for consumption of between 372 and 3,017 MT C yr^{-1}. Although there also are consumption rate estimates for other wetland herbivores such as Columbian white-tailed and black-tailed deer (8 to 11 MT C yr^{-1}), only an inestimable portion of that plant biomass actually originates from estuarine wetland habitats; other herbivores such as mice and voles, insects, and dabbling ducks (particularly mallards) undoubtedly consume a measurable portion of marsh plant biomass each year but estimates are not available.

Deposit Feeding

While the magnitude of living and non-living carbon potentially available to the deposit-feeding benthos might be estimable, the rates and efficiencies of its consumption and assimilation is difficult to measure under the best of circumstances (Miller and Mann 1973). In particular, recycling of fecal matter, resuspension of sedimented organics, and loss of dissolved organic matter complicate accurate assessment of energy flow through marine benthic assemblages (Mann 1969, Crisp 1971). No such energetic measurements were included in any of the CREDDP studies involving deposit-feeding consumer organisms and there is not sufficient data in the literature to estimate consumption by summation of documented consumption rates of the various taxa. Thus, at best, we can only backcalculate from total production estimates using literature information on ecological efficiencies. A number of authors (McNeil and Lawton 1970, Tait 1972, Steele 1974, Mann 1982) have suggested that, in general, approximately 70% of food consumption is used for respiration, 20% for secondary production, and 10% is egested unassimilated. However, variation in metabolic efficiency is considerable among taxa, but tends to converge on an assemblage or community level. Given this gross conversion efficiency and the estimates of deposit-feeding consumer production in the estuary (see Chapter 8), 1,943.30 MT C yr^{-1} is estimated to be consumed as a resource input into this subsystem of Consumption Processes.

Suspension Feeding

Within the water column, phytoplankton constitute the primary resource input to consumption processes by suspension-feeding zooplankton. Although actual consumption rate estimates were not generated during pelagic zooplankton studies, direct measurements (disappearance of 14C-labelled phytoplankton) of grazing rates by common surface water taxa (mixed copepods, *Bosmina longirostris*, and *Daphnia* spp.) upon phytoplankton were made in order to evaluate the loss of water column primary producers to consumption processes (see Section 7.1.1). Daily phytoplankton carbon removal by zooplankton grazing was estimated from data in Table 7.19. Consumption ranged from 0.05 mgC m^{-3} d^{-1} in January to 5.91 mgC m^{-3} d^{-1} in May. Assuming that these daily zooplankton consumption rates are applicable over all depth regions deeper than -0.3 MLLW in the main body of the estuary above the Entrance Region, extrapolation by these water volume values yielded estimates of between 2.4 MT C mo^{-1} (January) and 284.7 MT C mo^{-1} (May). Expanded to a yearly rate, approximately 1,042.5 MT C yr^{-1} of phytoplankton carbon is annually consumed by pelagic zooplankton in the estuary. Comparison with the estimated annual net phytoplankton production (28,143 MT C yr^{-1}; Table 7.24) indicates that only a minor (3.7%) proportion of the water column primary production is removed by these suspension feeders.

Predation

Benthic Infauna. While prey composition and consumption rates of *Eteone* spp., *Nephtys californiensis*, and *Eogammarus confervicolus* could not be evaluated directly in the studies, the literature indicates that they forage upon the smaller, meiofaunal components of the benthos, including other benthic infauna and epibenthic zooplankton such as nematodes, polychaetes, and harpacticoid copepods (see summaries by Fauchald and Jumars 1979 and Simenstad et al. 1979). Backcalculation from the annual production rate estimate for this component (Table 8.3) suggests that approximately 306 MT C yr^{-1} is consumed by predatory infauna in the estuary.

Epibenthic Macroinvertebrates. Through stomach contents analysis, Simenstad (1984) indicated that, although motile macroinvertebrates in the estuary were omnivorous, most of their diet was composed of benthic and epibenthic meiofauna as the diet composition varied considerably by season and location in the estuary. For example, a composite summary of all *Neomysis mercedis* examined from June 1980 samples indicated that rotifers were the numerically prevalent food organism (36.8% of total), followed by diatoms (12.5%) and cladocerans (primarily *Bosmina* sp.; 18.4%), during the high flow season (Table 7.45). A temporal composite of all *Neomysis* examined from Youngs Bay, however, indicated that

Table 7.45. Numerical composition (%) of food organisms consumed by *Neomysis mercedis* and *Crangon franciscorum* in the Columbia River Estuary, March 1980 - July 1981; n = number of stomachs examined. (Data from Simenstad 1984.)

Taxa	Principal Life History Stages	Numerical Composition (% of mean density)		
Rotifera	adults			2.7
Cladocera				4.7
Daphnidae			1.3	
Daphnia spp.	juveniles	0.7		
D. pulex Leydig	juveniles→adults	0.1		
D. rosea Sars	"	0.2		
D. galeata Sars	"	0.1		
D. retrocurva Forbes	juveniles	0.3		
D. parvula Fordyce	adults	<0.1		
Bosmidae			2.5	
Bosmina longirostris O.F. Muller	nauplii→adults	2.5		
Ostracoda			2.4	
Limnocytheridae	"		1.8	
Limnocythere Brady sp.	"	1.8		
Copepoda	"			76.4
"	nauplii		18.4	
Calanoida	nauplii→adults		17.7	
"	nauplii & adults	4.5		
Temoridae	copepodids→adults		12.2	
Epischura nevadensis Lilljeborg	adults	<0.1		
Eurytemora affinis (Poppe)	copepodids→adults	12.2		
Harpacticoida	nauplii→adults		34.9	
"	nauplii & copepodids	0.3		
Canuellidae			8.7	
Scottolana canadensis (Willey)	copepodids→adults	8.5		
Ectinosomatidae	"		17.5	
Microsetella Brady and Anderson sp.	adults	<0.1		
Ectinosoma Boeck sp.	copepodids→adults	0.1		
Tachidiidae			5.3	
Microarthridion littorale (Poppe)	"	2.6		
Tachidius Lillheborg sp.	copepodids	<0.1		
T. (Neotachidius) triangularis Shen and Tai	copepodids→adults	1.9		
Giesbrecht	"	0.3		
Canthocamptidae			2.2	
Bryocamptus Chappuis sp.	adults	0.5		
Mesochra lilljeborgi Boeck	"	<0.1		
M. alaskana M.S. Wilson	"	<0.1		
M. pygmaea (Claus)	"	<0.1		
Attheyella Brady sp.	"	1.7		
Cyclopoida	nauplii→adults		5.3	
Cyclopidae	copepodids→adults		5.1	
Halicyclops Norman sp.	"	<0.1		
Cyclops O.F. Muller sp.	"	1.3		
C. vernalis Fischer	"	1.2		
C. bicuspidatus thomasi S.A. Forbes	"	<1.9		
Mesocyclops edax (S. A. Forbes)	adult	0.1		
Paracyclops fimbriatus poppei (Rehberg)	copepodids adults	0.1		
Oithona Baird sp.	"	0.1		
O. similis Claus	adult	<0.1		

predation upon epibenthic meiofauna, particularly harpacticoid copepods such as Ectinosomidae (41.6%) and Scottolana canadensis (37.9%), was more typical of mysids on the tidal flats in that region of the estuary.

Crangon franciscorum also illustrated similar temporal/spatial variability, although not in the same patterns. Sand shrimp collected from throughout the estuary in August 1980 had fed principally upon Scottolana canadensis (61.0%) and secondarily upon diatoms (21.4%). Shrimp collected from Youngs Bay throughout the 18-month sampling period appeared to feed on the same two food resources but numerical composition had reversed to 62.6% diatoms and 22.7% Scottolana.

Qualitative analyses of juvenile Dungeness crab from the lower reaches of the estuarine mixing zone indicate that they are carnivorous upon macroinvertebrate components of the benthic infauna and epifauna, including Corophium sp., Neomysis mercedis, Cancer magister, barnacles (Balanus cypris), and unidentifiable bivalve molluscs and fish.

Definitive consumption rate estimates for these motile macroinvertebrates which could be extrapolated to the Columbia River Estuary populations were not found in the literature. Kuipers and Dapper (1981) provide an estimate of 2.7 gC m^{-2} yr^{-1} for juvenile Crangon crangon over a tidal flat in the Dutch Wadden Sea. The size-age structure of that population was significantly different from the Columbia River Estuary population. Therefore, backcalculation from production (Chapter 8) using a gross conversion efficiency of 15-20% (of ingested biomass) provides the only indication of consumption by epibenthic macroinvertebrate predators over the estuary as a whole, i.e. 109.8 to 146.47 MT C yr^{-1}.

Fishes. Based upon the Index of Relative Importance (IRI) criteria of prey importance (see Pinkas et al. 1971 and Simenstad et al. 1979 for an explanation of the IRI), Bottom et al. (1984) described seven generalized habitat feeding categories (Table 7.46): two pelagic planktivore groups which discriminate juvenile smelts, Pacific herring, and American shad from yearling and older smelt and shad; two epibenthic groups which discriminate between the juvenile salmonids and the more opportunistic threespine stickleback and shiner perch; and three demersal groups which separate the macrocrustacean-consumers such as Pacific tomcod, prickly and Pacific staghorn sculpin from the juvenile and older English sole and starry flounder.

Comparison of the food habits data with the seasonal (cluster) structure of the fish assemblages also indicated discrete feeding assemblages which generally corresponded to the taxa cluster groups (Tables 7.47-7.49). During the high flow season (Table 7.47) one or possibly two feeding assemblages were represented by four cluster groups (#'s 4,6,7,& 8), the first two of which were common in the mid- and lower (downriver) estuary purse seine collections and the upper (upriver) estuary trawl collections. American shad (cluster #6) occurred throughout the estuary but juvenile sockeye salmon and cutthroat trout (#7) were confined to the upper estuary. Three cluster groups (#'s 1, 2, & 3) correlated with two demersal feeding assemblages. Demersal predators and omnivores in the mid- and upper estuary and

Table 7.46. Fish and prey taxa comprising seven generalized feeding categories of predatory fishes during CREDDP investigations in the Columbia River Estuary, 1980-1981 (from Bottom et al. 1984).

FEEDING CATEGORY	FISH TAXA	PREDOMINANT PREY TAXA
Pelagic planktivores (mixed) (micro- and macrozooplankton)	Longfin smelt (1)* American shad (1&2+)	Calanoid & Harpacticoid copepods, *Corophium salmonis*, *Neomysis mercedis*; *Eogammarus*, *Daphnia***
Pelagic planktivores (microzooplankton)	Longfin smelt (0) American shad (0) Pacific herring (0&1)	Calanoid & cyclopoid copepods, *Daphnia*, *Bosmina*; harpacticoid copepods, *Neomysis mercedis*
Epibenthic-neustonic feeders (amphipod-insect)	Chinook salmon (0&1) Coho salmon(1)	Adult dipteran insects, *Corophium salmonis* & *C. spinicorne*, *Daphnia*; Chironomid larvae
Epibenthic browsers (amphipod-copepod)	Threespine stickleback Shiner perch (0&1)	*Corophium salmonis*, *Daphnia*, harpacticoid, calanoid & cyclopoid copepods; *Eogammarus*, *Gnorimosphaeroma*
Demersal predators (crustacean fish)	Pacific tomcod Prickly sculpin Staghorn sculpin	*Corophium salmonis*, *Crangon franciscorum*, *Eogammarus*; *Neomysis mercedis*, tomcod, northern anchovy, calanoid copepods, *Cancer magister*
Demersal planktivores (epibenthic zooplankton)	Starry flounder (0) English sole (0)	Harpacticoid, calanoid & cyclopoid copepods, polychaetes; *Eogammarus*, *Corophium salmonis*
Demersal Omnivores (crustacean, clam, polychaete)	English sole (2+) Starry flounder (1&2+)	*Corophium salmonis*, *Archaeomysis grebnitzkii*, *Macoma balthica* *Eogammarus*, *Mya arenaria*; polychaetes, *Neomysis mercedis*

* Numbers in parentheses indicate age class (in years) of fish.

**Prey taxa listed after semicolon are of secondary importance.

Table 7.47. Predominant (three highest contributors to total Index of Relative Importance; see text) prey of major fish predators, by cluster group, during high flow season 1980, in the Columbia River Estuary.

IRI (PERCENT)

░ 0.5 - 25
▒ 26 - 50
▓ 51 - 75
█ >75

PREDATOR	CLUSTER GROUP	N	Copepoda	Calanoida	Harpacticoida	Cyclopoida	*Bosmina longirostris*	Amphipoda	*Corophium salmonis*	*Corophium spinicorne*	*Eogammarus* sp.	*Saduria entomon*	Cumacea	Mysidacea	*Archaeomysis grebnitzkii*	*Neomysis mercedis*	*Crangon franciscorum*	Insect adults	*Corbicula manilensis*	*Macoma balthica*	Fish	DIGESTED (%)	OTHER (%)
Staghorn sculpin	I	120							▓							░					░	13.8	9.6
Starry flounder (1)		98		░					█													11.3	1.2
Starry flounder (2)		55							▓		░									░		21.2	3.6
Shiner perch (1)		6									█			░								0.9	0
English sole (0)		29		▒	░								░									6.3	17.8
Peamouth	II	-																				-	-
Prickly sculpin		82							█	░		░										10.4	2.1
Pacific tomcod	III	66									█				░		░					5.7	11.2
Snake prickleback		8		▓											░							19.9	9.5
Butter sole		13													█						░	11.7	0.6
English sole (1)		15						░							█					░		4.9	1.0
Pacific sand lance	IV	8		█			░															5.5	1.6
Speckled sanddab		-																				-	-
Shiner perch (0)		-																				-	-
Pacific herring (0)		12		█	░													░				11.3	2.6
Chinook salmon (1)	V	160							▓	░								░				10.3	5.4
Coho salmon		179							▓	░								░				23.9	4.1
Steelhead trout		81							░									░	░			67.1	8.1
Chinook salmon (0)		275							▓	░								░				15.0	5.9
Threespine stickleback		-																				-	-
American shad (1)	VI	132	░	▒					░													54.4	2.3
American shad (2)		-	░	░																		79.8	2.7
Sockeye salmon	VII	15	░	▒		░																29.9	3.4
Cutthroat trout		6							▒	░								▒				22.3	0.9
Longfin smelt	VIII	72		█					░							░						3.0	8.5
Pacific herring (1)		12		█	░																	11.3	2.6
Surf smelt		37		█	░																	6.8	2.0
Chum salmon	IX	9		▒			░											▒				12.6	5.6
Whitebait smelt	X	-																				-	-
Anchovy		-																				-	-

Table 7.48. Predominant (three highest contributors to total Index of Relative Importance; see text) prey of major fish predators, by cluster group, during low flow season 1980, in the Columbia River Estuary.

IRI (PERCENT)

- ░ 0.5-25
- ▒ 26-50
- ▓ 51-75
- █ >75

PREDATOR	CLUSTER GROUP	N	Polychaeta	Calanoida	Harpacticoida	Cyclopoida	*Daphnia*	*Bosmina longirostris*	*Corophium salmonis*	*Eogammarus* sp.	*Paraphoxis milleri*	*Archaeomysis grebnitzkii*	*Neomysis mercedis*	*Crangon franciscorum*	Insect parts	*Macoma balthica*	Fish	DIGESTED (%)	OTHER (%)
Longfin smelt (0)	I	56		▓		░	░											13.6	3.3
Longfin smelt (1)		195		█	░								░					7.8	1.3
Pacific tomcod		180		▒						░				▒				12.4	-
Snake prickleback		-																0	-
English sole (0)		67	░		░											░		55.0	2.3
Sand sole		-																-	-
Starry flounder (1)		97							█							░		15.5	3.2
Starry flounder (2)		39							░	░						▒		31.6	10.7
Shiner perch (1)	II	16			▒		░										░	26.8	6.8
Staghorn sculpin		217							▒					░			░	24.0	7.1
Starry flounder (0)		101				░			█									9.8	1.3
Shiner perch (0)		30		▒	░				░									58.1	3.6
Pacific lamprey	III	-																-	-
White sturgeon		15							▓				░			░		20.8	2.4
Northern anchovy	IV	30		░	▒	░												36.7	8.5
Whitebait smelt		7	░	█													░	0	0
Spiney dogfish		-																-	-
English sole (1)		9			░						░	░						73.8	1.1
Pacific herring (0)	V	119		▒		░	▒											19.3	2.3
American shad (1)		100		▒	░		░											64.2	2.2
Pacific herring (1)		18		▒		░	░											59.9	0.8
Surf smelt		49		▒		░	▒											12.8	0.6
American shad (2)		11		▒	░								░					27.3	12.8
Chinook salmon (0)	VI	432					█								░		░	8.0	5.7
Peamouth		13							░									93.0	0
Threespine stickleback		9		░		▒	▒											16.5	0
Cutthroat trout	VII	-																-	-
Largescale sucker	VIII	-																-	-
Prickly sculpin		103							█				░	░				20.4	1.4
American shad (0)		40		▒			░	░										41.0	1.5

Table 7.49. Predominant (three highest contributors to the total Index of Relative Importance; see text) prey of major fish predators, by cluster group, during fluctuating flow season 1980 - 1981, in the Columbia River Estuary.

IRI (PERCENT)

░ 0.5 – 25
▒ 26 – 50
▓ 51 – 75
█ > 75

PREDATOR	CLUSTER GROUP	N	Polychaeta	Calanoida	Harpacticoida	*Daphnia* sp.	*Corophium salmonis*	*Eogammarus* sp.	Cumacea	*Neomysis mercedis*	*Crangon franciscorum*	Diptera (adult)	Oligochaeta	*Mya arenaria*	*Macoma balthica*	Fish	DIGESTED (%)	OTHER (%)
American shad (1)	I	119		▒			░			░							49.3	4.7
Longfin smelt (1)		108		▒			▒			░							0.1	9.7
Eulachon		4	░							░							47.8	17.2
Threespine stickleback		75		░			▓										18.9	2.0
Staghorn sculpin	II	87					▓	░								░	2.3	5.3
Starry flounder (2)		49					▓							░	░		7.6	4.8
Starry flounder (1)		44					█						░				5.0	0.5
Prickly sculpin		56					█									░	2.1	1.0
Pacific tomcod	III	50		░				▓			░						1.7	8.3
Snake prickleback		21		░	▓			░									12.4	.02
English sole (1)		17	░					░	░					░			35.7	15.1
Butter sole		–															—	—
American shad (2)	IV	–															—	—
Surf smelt		14	░	░		░											58.2	0.9
Northern anchovy (1)	V	–															—	—
Sand sole		20		░				░		░						░	2.4	23.7
Whitebait smelt		–															—	—
Chinook salmon (0)	VI	92					▓			░		░					2.2	22.6

peripheral bays consumed Corophium salmonis and Eogammarus and, to a lesser extent, calanoid copepods and Neomysis mercedis. Demersal predators in the mid- to lower estuary (#3) foraged specifically upon the mysid Archaeomysis grebnitzkii.

During the low flow season (Table 7.48), feeding assemblages were more diverse and diet overlap greater than during the other seasons. Pelagic planktivores common to the mid- and lower water column habitats of the estuary (cluster #'s 1, 4, 5, & 6) preyed upon calanoid, cyclopoid, and harpacticoid copepods and cladocerans (Daphnia). Four fish clusters common to the mid- and lower regions of the estuary grouped epibenthic- and demersal-feeders (#1, 2, 3, & 8), most of which fed extensively upon C. salmonis. In addition, fish from cluster #2 (except Pacific staghorn sculpin) fed upon all copepod taxa; Pacific staghorn sculpin and yearling shiner perch ate other fish; and yearling and adult starry flounder and white sturgeon preyed upon Macoma balthica.

In the fluctuating flow season (Table 7.49), two clusters (#'s 1 & 4) identified pelagic and epibenthic planktivores from the mid-estuary and associated peripheral bay habitats which fed upon calanoid copepods and Daphnia (2^+ [two year old] American shad and surf smelt) in addition to epibenthic C. salmonis and Neomysis mercedis (yearling American shad and longfin smelt, eulachon, and threespine stickleback). Three clusters (#'s 2, 3, & 5) generally distinguished two demersal feeding assemblages. Cluster #2 (Pacific staghorn sculpin, starry flounder, prickly sculpin) included fish from demersal slope habitats in mid- and upper estuary regions which fed primarily upon C. salmonis and less so on bivalves (Mya arenaria, Macoma balthica) and fish. Tomcod, snake prickleback, and English and sand sole in the mid- and lower regions of the estuary fed on a diverse array of epibenthic (and possibly pelagic) crustaceans (harpacticoid and calanoid copepods, Eogammarus), and benthic infauna (polychaetes, Mya arenaria).

General feeding rates were indicated by the mean wet weight of the stomach contents as a percentage of the body wet weight (Index of Feeding Intensity, IFI; McConnell et al. 1983). These rates were quite variable among collection methods, regions, and habitats of the estuary, but generally fell between 0.2% and 0.4% (Figure 7.64). The variability, however, suggested several interesting patterns. Demersal fishes captured in the channel bottom habitats not only had higher IFI values (0.3% to 0.7%) than fish captured in the water column and demersal slope habitats, but there was also a definite trend toward higher relative stomach contents biomass in the central region of the estuary (RM-10 to RM-20). There is also a slight indication of higher relative stomach contents biomass in water column fishes in mid-estuary but the relationship is probably not significant. Demersal slope fishes show increasing relative stomach contents biomass from the upper reaches of the tidal-fluvial zone toward the estuary, with one of the highest reported IFI values (0.9%) at the lowest end of that zone. The highest IFI value (1.0%), however, occurs in the estuarine mixing zone.

Consumption rates of the estuary's fish predators are indirectly available from two sources, the growth rates estimated for five species

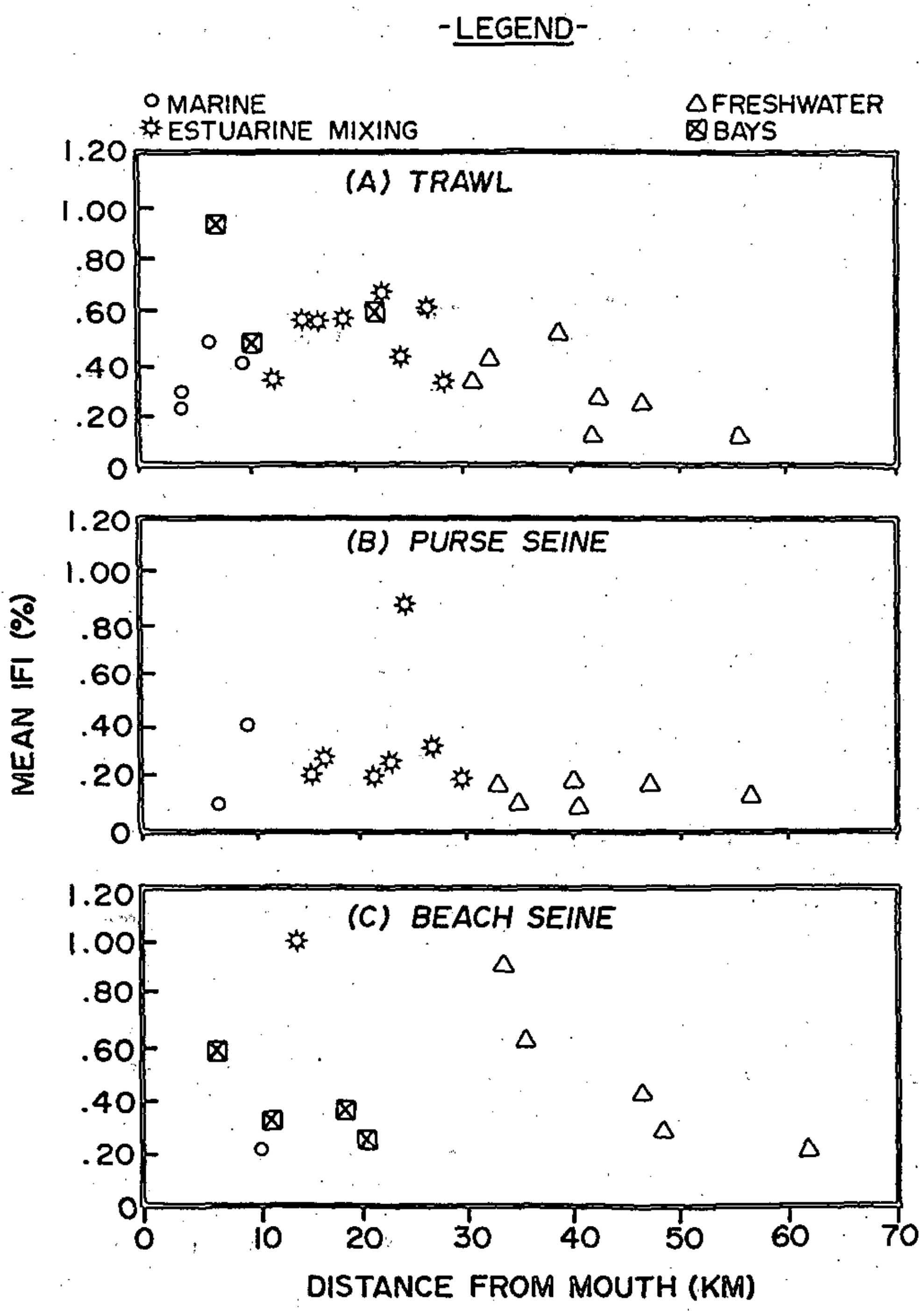


Figure 7.64. Mean weight of stomach contents as a percentage of body weight (IFI) for all fish analyzed for stomach contents at each station during CREDDP studies in the Columbia River Estuary. Data is presented by sampling method (A, trawl; B, purse seine; C, beach seine) which corresponds to channel bottom, water column, and demersal slope, respectively (from Bottom et al. 1984).

(McConnell et al. 1983) and extrapolation of feeding rates using assumptions of gastric evacuation. Bottom et al. (1984) generated consumption rate estimates for ten fish taxa/life history stages using one or both methods (Table 7.50). This comparison indicated that estimated consumption rates of subyearling English sole, subyearling and yearling starry flounder, yearling Pacific herring, and subyearling longfin smelt during high and low flow seasons were often less than could be accounted for by average daily growth rates because gross efficiency (growth/consumption) exceeded 100% for demersal species. Higher consumption rates were estimated for yearling and subyearling Pacific herring, yearling American shad, and longfin smelt during these seasons, resulting in gross efficiency estimates of 37%, 26%, 43%, and 43%, respectively. Relative to literature data on conversion rates, Bottom et al. (1984) concluded that consumption by demersal flatfishes was underestimated from two- to fourteen-fold, while estimates for winter consumption were more accurate. Discrepancies were also noted for pelagic species such as yearling Pacific herring and subyearling longfin smelt during the summer, which were underestimated by four- to ten-fold.

The ratio of the two consumption estimates (observed growth rates, C_g/estimated consumption rate, C_e; Table 7.50) was used to correct the daily ration estimates (C_e) for the seasonal assemblages (Table 7.51-7.53) by factors between 20% and 30% (Table 7.51). These consumption rates were on the order of 1%-4% body weight d^{-1} in the fluctuating and high flow seasons and 2%-10% body weight d^{-1} for pelagic species; 0.5%-2% body weight d^{-1} in winter and 2%-6% in spring and summer for demersal species; and 0.5%-6% body weight d^{-1} in the spring for epibenthic-feeding fishes.

This summary suggested that consumption rates of predatory fishes in the estuary may be somewhat lower than reported for the same or similar taxa/life history stages in other estuarine or nearshore marine ecosystems. For instance, estimates of daily ration for juvenile pink and chum salmon in other Pacific Northwest estuaries and coastal environs typically range from 10% to 16% body weight d^{-1} (LeBrasseur 1969; Parsons and LeBrasseur 1970; Healey 1979; Godin 1981) but have been estimated to be as high as 20%-30% (Simenstad et al. 1980) and about 40% (Godin 1981). Controlled physiological experiments with a variety of juvenile salmonids (principally sockeye [Oncorhynchus nerka]) indicates that maintenance rations (providing no growth) at 10°C are approximately 1% to 2% (Brett 1979). Although daily ration data is generally lacking for other comparable fish taxa in the region's estuaries, estimates for a number of freshwater and marine taxa in the same size range as the fish discussed by Bottom et al. (1984) also suggest that maintenance rations generally fall in the same range (i.e., 1% to 5%; Davis and Warren 1971; Kitchell et al. 1977; Thorpe 1977; Nakashima and Leggett 1978; Brett 1979).

A very rough estimate of the total annual consumption rate by predatory fish in the estuary can be made using an average daily consumption rate of 5% body weight d^{-1} multiplied by the average annual standing crop (59.48 MT C; see Chapter 8), or 1,085.51 MT C yr^{-1}.

Table 7.50. Comparison of consumption rate estimates calculated from mean estimated daily ration and from observed growth rates (Cg); see Bottom et al. (1984) for assumptions and details of computations.

SPECIES	ESTIMATED CONSUMPTION Ce (%/day)	MEAN GROWTH Gw (%/day)	GROSS EFFICIENCY Gw/Ce (%)	PREDICTED CONSUMPTION Cg (Efficiencies)				CORRECTION FACTOR Cg/Ce (Efficiencies)			
				.10	.20	.30	.40	.10	.20	.30	.40
English sole (0)											
April-June	.55-1.10	1.18	107-214	11.8	5.9	3.9	3.0	10.7	5.4	3.5	2.7
July-October	.55-1.10	.72	65-131	7.2	3.6	2.4	1.8	6.5	3.3	2.2	1.6
English sole (1)											
February-March	.51-1.01	.22	22-43	2.2	1.1	.7	.6	2.2	1.1	.7	.6
April-June	.90-1.20	1.01	84-112	10.1	5.0	3.4	2.5	8.4	4.2	2.8	2.1
Starry flounder (0)											
July-October	1.10-1.47	2.06	140-187	20.6	10.3	6.9	5.2	14.0	7.0	4.7	3.5
Starry flounder (1)											
February-March	.23-.34	.21	62.91	2.1	1.1	.7	.5	6.2	3.1	2.0	1.5
April-June	.46-.92	.75	82-163	7.5	3.8	2.5	1.9	8.2	4.1	2.7	2.1
July-October	.41-.55	.71	129-173	7.1	3.6	2.4	1.8	13.0	6.5	4.4	3.3
Starry flounder (2+)											
February-March	.28-.41	.10	24-36	1.0	.5	.3	.2	2.4	1.2	.7	.5
April-June	.46-.92	.75	82-163	7.5	3.8	2.5	1.9	8.2	4.1	2.7	2.1
American shad (1)											
February-March	3.32	.08	2.4	.8	.4	.3	.2	.24	.12	.09	.06
April-June	4.08	1.76	43	17.6	8.8	5.9	4.4	4.2	2.1	1.4	1.1
July-August	1.10-1.44	.73	51-66	7.3	3.6	2.4	1.8	5.0	2.5	1.7	1.2
Pacific herring (0)											
July-October	1.96	.52	26	5.2	2.6	1.7	1.3	2.6	1.3	.9	.7
Pacific herring (1)											
May-June	1.19	.44	37	4.4	2.2	1.5	1.1	3.6	1.8	1.3	.9
July-October	.34-.44	.74	168-218	7.4	3.7	2.5	1.8	16.8	8.4	5.7	4.1

Table 7.50. (Continued).

SPECIES	ESTIMATED CONSUMPTION Ce (%/day)	MEAN GROWTH Gw (%/day)	GROSS EFFICIENCY Gw/Ce (%)	PREDICTED CONSUMPTION Cg (Efficiencies)				CORRECTION FACTOR Cg/Ce (Efficiencies)			
				.10	.20	.30	.40	.10	.20	.30	.40
Longfin smelt (0)											
July-October	.42-.55	.88	160-210	8.8	4.4	2.9	2.2	16.0	8.0	5.3	4.0
Longfin smelt (1)											
February-March	2.04	.26	.13	2.6	1.3	.9	.6	1.3	.6	.4	.20
April-June	1.36	0	0	0	0	0	0	0	0	0	0
July-October	.60-.77	.26	34-43	2.6	1.3	.9	.6	3.4	1.7	1.2	1.6

[a] Cp and Ce/Cp are calculated for each of 4 levels of conversion efficiency (.10,.20,.30, and .40).

[b] maximum Ce values used to calculate Cp/Ce.

Table 7.51. Estimated consumption rates for species in each feeding assemblage in the Columbia River Estuary calculated from growth rates (Cp) and/or correction factors applied to Ce (see Table 7.54). Lower estimate = (le), and upper estimate = (ue).

	Range of Consumption (%/day)	Method of Estimation	Correction Factor Applied to Ce	Total Range by Assemblage
I. WINTER ASSEMBLAGES				
A. Pelagic 1				
American shad (1)	.3-3.3	B		0-3.6
Longfin smelt (1)	.9-2.0	A,B		
Eulachon	0-1.4	A,B		
Threespine stickleback	.8-3.6	A		
B. Pelagic 2				
American shad (2+)	no estimate			
Surf smelt	.9-2.4	A,C	.4 (le)	.9-4.9
Whitebait smelt	2.0-4.9	A,C	.4 (le)	
Northern anchovy	no estimate			
C. Demersal 1				
Staghorn sculpin	.5-2.3	C	.7-3.1	
Starry flounder (1)	.7-1.1	B		.3-2.3
Starry flounder (2+)	.3-.5	B		
Prickly sculpin	.4-1.6	C	.7-3.1	
D. Demersal 2				
Pacific tomcod	.7-14.6	C	.7-3.1	
Snake prickleback	no estimate			.3-14.6
English sole (1)	.7-1.1	B		
Sand sole	.9-2.3	C	.7-1.1	
Cutter sole	.3-.8	C	.7-1.1	
E. Epibenthic-surface				
Chinook salmon (0)	.3-1.0	C	.7-1.1	.3-1.0
II. SPRING ASSEMBLAGES				
A. Pelagic 1				
Pacific sandlance	no estimate			
Pacific herring (0)	2.5-3.5	C	1.3-1.8	3.-4.4
Pacific herring (1)	1.2-2.2	A,B		
Longfin smelt (1)	0-1.4	A,B		
Surf smelt	.9-1.4	C	1.3-2.1	
Whitebait smelt	2.9-4.4	C	1.3-2.1	
Northern Anchovy (1)	.3-.6	A,C	2.1 (ue)	
Chum salmon	no estimate			
B. Pelagic 2				
American shad (1)	4.1-8.8	A,B		1.4-8.8
American shad (2+)	1.4-2.1	C	1.4-2.1	
Sockeye salmon	no estimate			

Table 7.51. (Continued).

	Range of Consumption (%/day)	Method of Estimation	Correction Factor Applied to Ce	Total Range by Assemblage
C. Demersal 1				
Staghorn sculpin	2.5-5.0	C	2.7-5.4	1.8-5.9
Starry flounder (1)	2.5-3.8	B		
Starry flounder (2+)	2.5-3.8	B		
Shiner perch (1)	no estimate			
English sole (0)	3.9-5.9	B		
Prickly sculpin	1.8-3.7	C	2.7-5.4	
Peamouth	no estimate			
D. Demersal 2				
Pacific tomcod	2.2-12.9	C	2.7-5.4	2.2-12.9
Sualie prickleback	no estimate			
Butter sole	2.2-5.9	C	2.7-5.4	
English sole (1)	3.4-5.0	B		
Specked sanddab	no estimate			
Shiner perch	no estimate			
E. Epibenthic-surface				
Chinook salmon (0)	1.4-9.8	C	2.7-5.4	.6-9.8
Chinook salmon (1)	.6-3.4	C	2.7-5.4	
Coho salmon	.8-4.8	C	2.7-5.4	
Steelhead trout	.9-1.9	C	2.7-5.4	
Threespine stickleback	.6-7.3	A		
Cutthroat trout	no estimate			
II. SUMMER ASSEMBLAGES				
A. Pelagic 1				
Longfin smelt(1)	.9-1.3	B		.6-22.1
Northern anchovy (1)	5.5-22.1	A		
Whitebait smelt	.6-1.1	C	1.2-1.7	
B. Pelagic 2				
Pacific herring (0)	1.7-2.6	B		.8-9.2
Pacific herring (1)	2.5-3.7	B		
American shad (0)	2.7-8.8	A,C	2.5 (ue)	
American shad (1)	2.4-3.6	B		
American shad (2+)	1.2-2.2	C	1.7-2.5	
Surf smelt	.8-7.0	C	1.2-8.0	
Longfin smelt (0)	2.9-4.4	B		
Threespine stickleback	1.1-9.2	A		
Shiner perch (1)	no estimate			

Table 7.51. (Continued).

	Range of Consumption (%/day)	Method of Estimation	Correction Factor Applied to Ce	Total Range by Assemblage
C. Demersal-epibenthic				
Starry flounder (0)	6.9-10.3	B		.9-10.3
Starry flounder (1)	2.4-3.6	B		
Starry flounder (2+)	2.4-3.6	B		
Staghorn sculpin	2.7-8.7	C	2.2-7.0	
Shiner perch (0)	no estimate			
Prickly sculpin	.9-3.0	C	2.2-7.0	
White sturgeon	no estimate			
Peamouth	no estimate			
Largescale sucker	no estimate			
D. Demersal-omnivore				
English sole (0)	2.4-3.6	B		8.-17.0
English sole (1)	.8-1.2	B		
Sand sole	-			
Pacific tomcod	5.3-17.0	C	2.2-7.0	
Snake prickleback	no estimate			
E. Epibenthic-surface				
Chinook salmon (0)	3.0-9.7	C	2.2-7.0	3.0-9.7
Cutthroat trout	no estimate			

[a] Range in consumption estimated by the following methods:

A. Estimated from IFI values according to equation (1), Ce.

B. Estimated from growth rates assuming 20-30% gross conversion efficiency, Cp.

C. Estimated by applying a correction factor to Ce for species with no growth data. Correction factor represents the probable range in adjustment needed in Ce to account for growth rates found for other fishes in the same or similar feeding assemblage. Correction factors assume 20-30% conversion efficiencies.

Avifauna. Only generalized, qualitative feeding information is available on the feeding characteristics of predatory avifauna in the estuary, which was derived almost exclusively from literature information and correlation with the temporal and spatial distributions of assumed prey organisms in the estuary (Hazel et al. 1984).

Peeps were considered to prey extensively upon the high densities of *Corophium salmonis*, nematodes, and oligochaetes in the tidal flat habitats in the vicinity of Quinns Island, and Baker and Grays Bays during winter and spring. Hybrid gull nesting sites in the East Sand Island area possibly were associated with high densities of a number of fish species in the same area. Surf scoter predation on infaunal bivalves was correlated with high winter use of Baker Bay, where *Macoma* densities were relatively high, and in the Cathlamet Bay islands area, where *Corbicula* is also relatively abundant. Piscivorous common mergansers were most abundant in Baker Bay during the spring, summer, and winter when high densities of shiner perch, Pacific staghorn sculpin, starry flounder, English sole, and Pacific herring were periodically abundant; during the winter, their shift in abundance to the Knappton and Tongue Point areas correlated to longfin smelt densities. Western grebe, also piscivorous, maintained large populations in the vicinity of Grays Bay, Harrington Point, and Knappton during the winter, which also corresponded with periodically high densities of longfin smelt, starry flounder, Pacific herring, and juvenile salmonids. Double-crested and pelagic cormorants both occupied regions and habitats in the lower estuary which sustain high fish populations, specifically Cape Disappointment (all seasons), Trestle Bay (summer), and East Sand Island (autumn). Great blue herons, also piscivorous, occupied both Baker Bay and Youngs Bay although on a seasonally variable basis, i.e. more so Youngs Bay in the spring and summer; high densities of shiner perch, Pacific staghorn sculpin, and starry flounder were considered important prey resources of the herons in these regions.

Consumption rates were not estimated for these avifauna taxa. However, Hazel et al. (1984) listed literature values of consumption rates for nine taxa/life history stage groups which ranged between 10% body weight d^{-1} for mallards to 33% body weight d^{-1} for adult common mergansers. Assuming an average consumption rate of 15% body weight d^{-1}, a rough estimate of annual consumption by the estuary's avifauna would be between 0.3 and 0.6 MT C yr^{-1}.

Terrestrial and Aquatic Mammals. Merker and Fenton (1984) ranked scat remains of raccoon in the estuary in order of relative importance: crayfish; *Corbicula manilensis*; unidentified birds; Rosaceae fruit; and sculpin. Crayfish and *Corbicula* were assumed to be important throughout the year, while birds and fruits were more seasonally available. Consumption rate was estimated to be 23.25 MT wet weight day^{-1} or approximately 23.35 kgC day^{-1}, which corresponds to 8.52 MT C yr^{-1}.

Analysis of Canadian otter scats also indicated that crayfish were their principal dietary constituent, followed by sculpin, carp, unidentified fish, and starry flounder (Merker and Fenton 1984). Consumption rates were estimated to be approximately 3.76 to 4.47 kgC

day^{-1} or 1.37 to 1.63 MT C yr^{-1}.

Marine Mammals. Jeffries et al. (1984) utilized an elaborate combination of scat and intestinal tract analysis to determine the principal prey of sea lions and harbor seals in the estuary. These results, summarized in Tables 7.52-7.54, indicated that the prey of harbor seals in the estuary (and adjacent waters, due to the high movement rates of these pinnipeds) included a wide variety of jawless (lampreys) and bony fish, decapod crustaceans, and cephalopods (Table 7.54). The bony fish were the predominant prey on the basis of occurrence, including longfin smelt, Pacific staghorn sculpin, Pacific tomcod, English sole, starry flounder, snake prickleback, and Pacific herring (Table 7.53). Among the macroinvertebrate prey, cancrid crab and crangonid shrimp were the most common but many bivalve molluscs (unidentified but including *Corbicula manilensis*) were also frequently consumed (Tables 7.53 and 7.54). There was no indication of any seasonal pattern in the consumption (by occurrence) of invertebrates by harbor seals (Table 7.54).

Consumption could not be estimated directly from CREDDP data but could be extrapolated from the sea lion and harbor seal population estimates using McAlister's (1981) estimates of the daily energy requirement (assuming about 10 kcal g^{-1} C) of pinnipeds at 6°C--1.91 kgC sea lion^{-1} d^{-1} and 0.72 kgC harbor seal^{-1} d^{-1}. Extrapolating by the seasonal population estimates in the estuary (Table 7.48), consumption by sea lions in the estuary is estimated to be 69.55 MT C yr^{-1} and by harbor seals is 244.21 MT C yr^{-1}, or a total of 313.76 MT C yr^{-1} for these marine mammals.

Production

Population production is considered at two levels of biomass accumulation: (1) production relative to "growth" which is that part of the assimilated food or energy that is retained and incorportated in the biomass of the organisms; and (2) production relative to reproduction, which is that part of the absorbed energy released as reproductive bodies (Crisp 1971).

As a measure of both, production was measured directly only in the case of *Corophium salmonis* populations at two sites in the estuary, Grays Bay and Desdemona Sands (Holton et al. 1984). Monthly production estimates in these two divergent habitats also showed quite different trends in terms of magnitude and the period of peak production. The Grays Bay population was comparatively stable, increasing from production rates of less than 10 mgC m^{-2} d^{-1} during the fluctuating flow season to between 25 and 35 mgC m^{-2} d^{-1} during the high flow season and declining steadily into the low flow season (Fig. 7.65). In direct contrast, the more ephemeral population on Desdemona Sands first occurred in the habitat in March and increased rapidly (through recruitment of juveniles) through the high flow season and into the early period of the low flow season, reaching a maximum production of almost 90 mgC m^{-2} d^{-1} in July.

All other production estimates were generated using literature

Table 7.52. Scientific and common names of primary-type prey species identified in harbor seal scats, sea lion scats, and gastrointestinal tracts of stranded marine mammals collected in the Columbia River Estuary and adjacent waters, June 1980-April 1982. (Jeffries et al. 1984)

Prey Species	Family	Common Name	Harbor Seal Scats	Sea Lion Scats	Stranded Marine Mammals
Bony Fish (Robins et al. 1980):					
Allosmerus elongatus	Osmeridae	White smelt	X	X	X
Alosa sapidissima	Clupeidae	American shad	X		X
Ammodytes hexapterus	Ammodytidae	Pacific sand lance			X
Amphistichus rhodoterus	Embiotocidae	Redtail surfperch	X		X
Anoplopoma fimbria	Anoplopomatidae	Sablefish	X		X
Atheresthes stomias	Pleuronectidae	Arrowtooth flounder			X
Brachyistius frenatus	Embiotocidae	Kelp perch			X
Citharichthys sordidus	Bothidae	Pacific sanddab	X		X
Citharichthys stigmaeus	Bothidae	Speckled sanddab	X		
Clupea harengus pallasi	Clupeidae	Pacific herring	X		X
Cottus sp.	Cottidae	(Sculpin)			X
Cymatogaster aggregata	Embiotocidae	Shiner perch	X		X
Cyprinus carpio	Cyprinidae	Common carp	X		
Embiotocid	Embiotocidae	(Surfperches)	X	X	
Engraulis mordax	Engraulidae	Northern anchovy	X		X
Eopsetta jordani	Pleuronectidae	Petrale sole	X		X
Glyptocephalus zachirus	Pleuronectidae	Rex sole	X		X
Hemilepidotus sp.	Cottidae	(Irish lord)	X		
Hypomesus pretiosus	Osmeridae	Surf smelt	X		X
Icelus sp.	Cottidae	(Sculpin)	X		
Isopsetta isolepsis	Pleuronectidae	Butter sole	X		
Leptocottus armatus	Cottidae	Pacific staghorn sculpin	X	X	X
Lumpenus sagitta	Stichaeidae	Snake prickleback	X		
Lyopsetta exilis	Pleuronectidae	Slender sole			X
Merluccius productus	Merlucciidae	Pacific hake	X		X
Microgadus proximus	Gadidae	Pacific tomcod	X		X

Table 7.52. (continued)

Prey Species	Family	Common Name	Harbor Seal Scats	Sea Lion Scats	Stranded Marine Mammals
Microstomus pacificus	Pleuronectidae	Dover sole	X		X
Myctophid	Mytophidae	(Lanternfishes)			X
Oncorhynchus nerka	Salmonidae	Sockeye salmon	X		
Oncorhynchus tshawytscha	Salmonidae	Chinook salmon			X
Parophrys vetulus	Pleuronectidae	English sole	X		
Phanerodon furcatus	Embiotocidae	White seaperch			X
Pholis sp.	Pholidae	(Gunnel)	X		
Platichthys stellatus	Pleuronectidae	Starry flounder	X		
Pleuronectid	Pleuronectidae	(Righteye flounders)	X		
Poroclinus rothrocki	Stichaeidae	Whitebarred prickleback	X		
Psettichthys melanostictus	Pleuronectidae	Sand sole	X	X	X
Radulinus asprellus	Cottidae	Slim sculpin	X		
Rhacochilus vacca	Embiotocidae	Pile perch			X
Salmo bairdneri	Salmonidae	Steelhead trout	X	X	X
Sebastes spp.	Scorpenidae	(Rockfishes)	X		X
Spirinchus thaleichthys	Osmeridae	Longfin smelt	X		
Thaleichthys pacificus	Osmeridae	Eulachon	X	X	X
Theragra chalcogramma	Gadidae	Walleye pollock			X
Trichodon tricodon	Trichodontidae	Pacific sandfish	X		
Agnathans (Robins et al. 1980):					
Eptatretus sp.	Myxinidae	(Hagfish)	X		
Lampetra ayresi	Petromyzontidae	River lamprey	X		X
Lampetra tridentata	Petromyzontadae	Pacific lamprey	X	X	X
Lampetra sp.	Petromyzontidae	(Lamprey)	X		X
unident. agnathans		(Jawless fishes)	X		
Decapod crustaceans (NODC tax. code 1978):					
Callianassa sp.	Callianassidae	(Ghost Shrimp)	X		

Table 7.52. (continued)

Prey Species	Family	Common Name	Harbor Seal Scats	Sea Lion Scats	Stranded Marine Mammals
Cancer magister	Cancridae	Dungeness crab			X
Cancer sp.	Cancridae	(Crab)	X		
Crangon sp.	Crangonidae	(Crangon shrimp)	X	X	X
unident. crab			X		
unident. crustacean			X		
Cephalopods (Roper et al. 1969):					
Loligo opalescens	Loliginidae	Market squid	X		X
Octopoteuthis deletron	Octopoteuthidae	(Squid)			X
Octopus sp. (Benthic)	Octopodidae	(Benthic octopus)	X	X	X
Ommastrephid	Ommastrephidae	(Squid)			X
Onychoteuthis sp.	Onychoteuthidae	(Squid)			X
unident. cephalopod					X
unident. squid					X

Table 7.53. Frequency of occurrence of food remains, in phylogenetic order, identified in harbor seal scats collected in the Columbia River Estuary June 1980 - April 1982; n = 436 (Jeffries et al. 1984).

Taxon	Columbia River (n=436)
PHYLUM Mollusca (unident.)	
CLASS Gastropoda (unident.)	3
CLASS Bivalvia (unident.)	78
Heterodonta, Veneroida	
FAMILY Corbiculidae	
Corbicula manilensis	1
CLASS Cephalopoda	
Teuthoidea	
FAMILY Loliginidae	
Loligo opalescens	2
Octopoda	
FAMILY Octopodidae	
Octopus sp.	1
PHYLUM Arthropoda	
CLASS Crustacea (unident.)	72
Cirripedia, Thoracica (unident.)	2
Isopoda (unident.)	1
FAMILY Idoteidae (unident.)	1
Saduria entomon	2
Amphipoda	
FAMILY Corophiidae	
Corophium sp.	3
Corophium spinicorne	3
FAMILY Gammaridae (unident.)	
Eogammerus confervicolus	2
Decapoda (unident.)	1
Decapoda, Caridea	
FAMILY Crangonidae	
Crangon sp.	7
Decapoda, Anomura	
FAMILY Callianassidae	
Callianassa sp.	1
Decapoda, Brachyura	1
FAMILY Cancridae	
Cancer sp.	13

Table 7.53 (continued).

Taxon	Columbia River (N=436)
PHYLUM Chordata	
CLASS Agnatha (unident.)	7
ORDER Myxiniformes	
FAMILY Myxinidae	
Eptatretus sp.	3
ORDER Petromyzontiformes	
FAMILY Petromyzontidae	
Lampetra sp.	24
Lampetra ayresi	29
Lampetra tridentata	10
CLASS Osteichthyes	
ORDER Clupeiformes	
FAMILY Clupeidae	
Alosa sapidissima	2
Clupea harengus pallasi	13
FAMILY Engraulidae	
Engraulis mordax	92
ORDER Salmoniformes	
FAMILY Salmonidae	
Oncorhynchus nerka	1
Salmo Gairdneri	2
FAMILY Osmeridae	
Allosmerus elongatus	157
Hypomesus pretiosus	1
Spirinchus thaleichthys	25
Thaleichthys pacificus	36
ORDER Cypriniformes	
FAMILY Cyprinidae	
Cyprinus carpio	3
ORDER Gadiformes	
FAMILY Gadidae	
Merluccius productus	15
Microgadus proximus	39
ORDER Perciformes	
FAMILY Embiotocidae (unident.)	1
Amphistichus rhodoterus	2
Cymatogaster aggregata	5
FAMILY Trichodontidae	
Trichodon trichodon	2
FAMILY Stichaeidae	
Lumpenus sagitta	29
Poroclinus rothrocki	1
FAMILY Pholidae	
Pholis sp.	1
FAMILY Scorpaenidae	
Sebastes sp.	1

Table 7.53 (continued).

Taxon	Columbia River (n=436)
FAMILY Anoplopomatidae	
Anoplopoma fimbria	2
FAMILY Cottidae	
Hemilepidotus sp.	1
Icelus sp.	1
Leptocottus armatus	45
Radulinus asprellus	1
ORDER Pleuronectiformes	
FAMILY Bothidae	
Citharichthys sordidus	2
Citharichthys stigmaeus	4
FAMILY Pleuronectidae (unident.)	2
Eopsetta jordani	2
Glyptocephalus zachirus	2
Isopsetta isolepsis	3
Microstomus pacificus	1
Parophrys vetulus	13
Platichthys stellatus	18
Psettichthys melanostictus	5

Table 7.54. Occurrence (%) of invertebrates in harbor seal scats collected in the Columbia River Estuary June 1980 - April 1982; data pooled by month (Jeffries et al. 1984).

Taxon	1981-82 (n=30) Jan	1982 (n=15) Feb	1981-82 (n=9) Mar	1981-82 (n=33) Apr	1981 (n=19) May	1980-81 (n=22) Jun	1980-81 (n=115) Jul	1980-81 (n=69) Aug	1981 (n=72) Sep	1980 (n=12) Oct	1980 (n=16) Nov	1980 (n=24) Dec
Unident. fragments	36.7%		33.3%	51.5%	84.2%	45.5%	35.7%	44.9%	22.2%	50%	56.3%	37.5%
PHYLUM Mollusca												
Gastropoda (unident.)							1.7%	1.4%				
Bivalvia (unident.)	3.3%	22.2%	33.3%	3%		40.9%	30.4%	7.2%	33.3%	8.3%		
Corbiculidae												
Corbicula manilensis									1.4%			
PHYLUM Arthropoda												
Crustacea (unident.)	16.7%	6.7%		15.2%		36.4%	10.4%	17.4%	30.6%	8.3%	18.8%	12.5%
Cirripedia (Thoracica)							0.9%				6.3%	
Isopoda (unident.)								1.4%				
Idoteidae									1.4%			
Saduria entomon				3%								
Amphipoda												
Corophiidae												
Corophium sp.							0.9%	1.4%	1.4%			
C. spinicorne							2.6%					
Gammaridae												
Eogammerus confervicolus							0.9%					

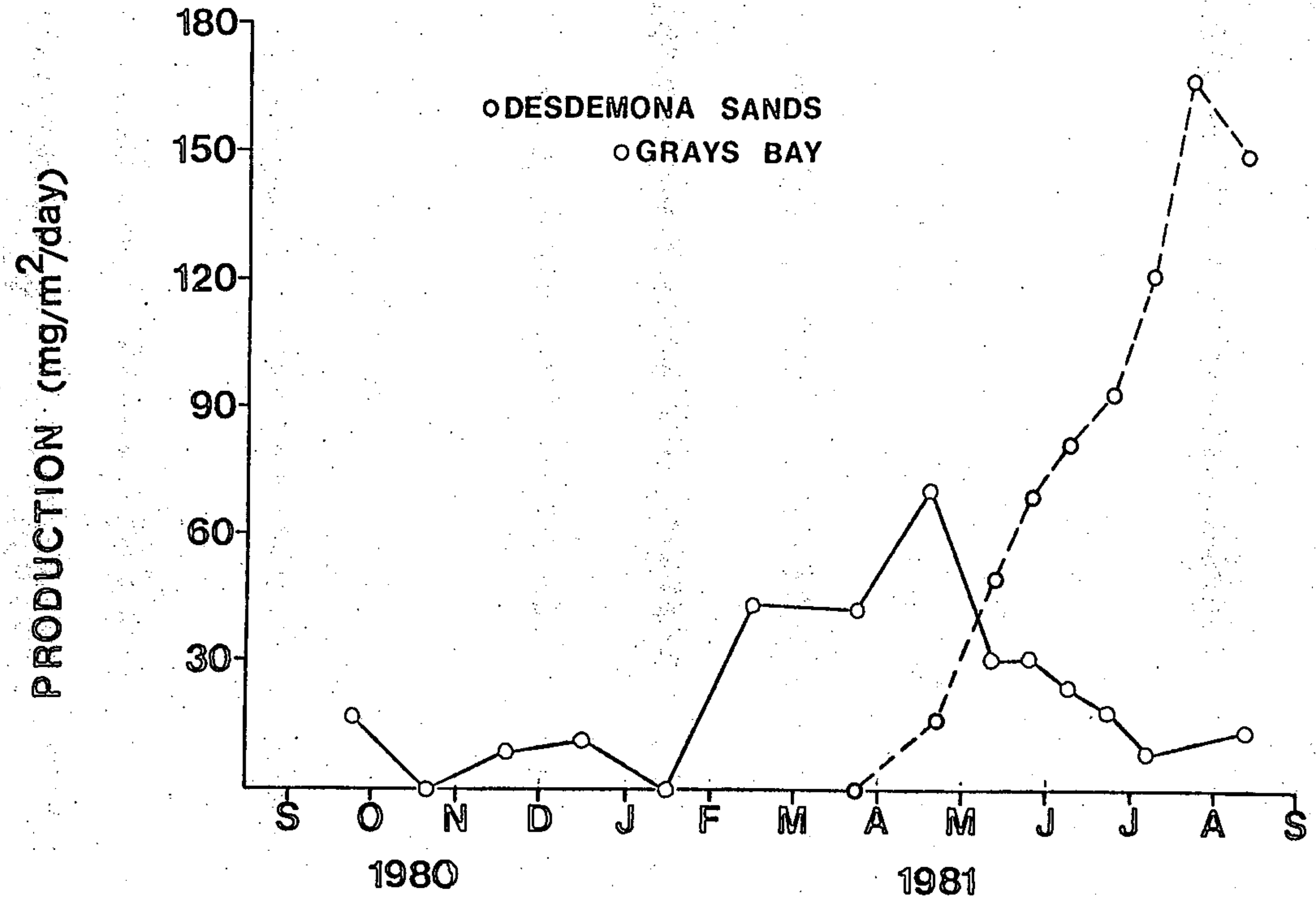


Figure 7.65. Daily production rate (mgC m^{-2} day^{-1}) of Corophium salmonis at two tidal flat habitats during CREDDP studies in the Columbia River Estuary, September 1980 - August 1981 (Holton et al. 1984).

values for the ratio of production to standing crop or biomass (P/B) and are tabulated by habitat and region in Chapter 8.

Process Generated Outputs

Respiratory Products

Respiratory products of Consumption Processes were not measured at either the organismal or community level during the studies. Literature data on the metabolic partitioning of energy (carbon) ingested by benthic organisms and communities suggest that, of the total amount ingested, approximately 70% is converted to respiratory products, 20% is actually converted to biomass (production), 10% is unassimilated egesta (McNeill and Lawton 1970, Dame 1972, Miller and Mann 1973).

Lasker's (1970) energy budget analysis of Pacific sardine, Sardinops caerulea, illustrated that respiratory losses increased from 81.5% to 97.9% over the six-year age span of the sardine; over the same period, energy assimilated for growth and reproduction (total production) declined from 18.5% to 1.0% and increased from 0% to 1.1%, respectively. Using 18.5%-81.5%, 10.0%-90.0%, and 7.5%-92.5% production-respiration relationships for larval, juvenile, and adult fish, and extrapolating from estimated annual production for the estuary (Chapter 8), it was estimated that 195.85 MT C yr^{-1} is respired by larval fish and between 257.25 and 366.70 MT C yr^{-1} is respired by juvenile and adult fish.

The lack of similar energy allocation information for avifauna and terrestrial, aquatic, and marine mammal predators makes it impossible to make estimates for these organisms. However, their respiration is output to the atmosphere and, as such, does not constitute a carbon input into the estuarine ecosystem but out of it.

Fecal Discharge

Although fecal discharge can constitute a significant output product of Consumption Processes in terms of the proportion of total carbon processed by a subsystem, this carbon flux out of the subsystems was not measured during any of these investigations. The literature indicates that at least suspension- and deposit-feeding zooplankters generate fecal pellets and pseudofeces amounting to between 20% and 30% of the ingested organic carbon (Cushing 1966, Tenore and Dunstan 1973, Tenore et al. 1973).

Dissolved Organic Matter

In some ways similar to non-respiratory output of organic carbon through extracellular release of dissolved organic matter (DOM; see Section 6.3.2), there is also evidence that losses of DOM can constitute significant terms in the energy budgets of estuarine and marine fauna (Miller and Mann 1973). This non-respiratory/egestion loss could occur during feeding, during defecation, or even through passive diffusion through the body surface (Mann 1982). Obviously, this is a potentially dynamic metabolic process which has yet to be quantified.

As the requisite laboratory experiments using organisms or assemblages from the estuary have not been conducted, it must be assumed that this unknown output is included in the combined respiration and egestion losses.

Non-process Generated Inputs and Outputs

Imports and Exports

Imports and exports of consumers involve both passive and active transport of consumer organisms into and out of the estuary. Considerable passive transport occurs with the extensive freshwater discharge of the Columbia River, as freshwater zooplankton are imported into the estuary via the same process as phytoplankton (see Section 7.1.7). Although not in the same magnitude, passive transport of marine zooplankton occurs as a function of the net tidal exchange. Unlike most of the primary producers, active (behavioral) mechanisms also account for much of the import and export of consumer organisms. Highly motile animals such as the migratory birds and marine mammals represent the extreme example, but the flux of juvenile anadromous Pacific salmon during their migration to the North Pacific Ocean also illustrates an active import-export process of resources and consumers; passage of the returning adult salmon through the estuary only represents resource import and export, as they do not feed by this stage of their migration. Active behavior also accounts for retention of consumer organisms within the estuary in the face of the strong transport forces (i.e., net flow downriver). For example, the estuarine calanoid copepod *Eurytemora affinis* is apparently able to maintain a viable, reproductive population within the estuary, probably by vertical migration into net upstream-moving water masses and out of net-downstream water masses (see Miller 1983 for review).

Wetland Herbivores. Although all wetland herbivores are essentially indigenous to the estuary, and theoretically constitute relatively closed populations, import could occur from movement of animals into the estuarine ecosystem from adjacent upland habitats or from upriver. Unfortunately, there are no estimates for such exogenous recruitment. Export from the system could also occur through similar movement and from mortality which results in removal from the system, primarily through trapping activities by man. Although, again, we have no estimates of wetland herbivore movement out of the system, Merker and Fenton (1984) provided estimates of the anthropogenic removal of animals through harvesting by trapping and hunting. These data (Table 7.55) suggest that approximately 22.4 MT yr^{-1} or 2.2 MT C yr^{-1} (assuming 10% C:wet weight ratio) of nutria, muskrat, and American beaver is directly exported from the estuary by trappers. There is also some natural mortality due to removal by adjacent (upland) predators which capture their prey within wetland habitats but export and consume them outside the estuary. Davison (1979, cited in Merker and Fenton 1984) reported coyote (*Canis latrans*) as killing between seven and eighteen deer fawns annually, a large percentage of which were probably removed from the estuary. Other (natural) mortality factors other than predation, e.g., disease, malnutrition, etc., are assumed to contribute to the Detrital Decomposition Process resource rather than export.

Table 7.55. Estimated removal of wetland herbivorous and predatory mammals from Columbia River Estuary due to harvesting (Merker and Fenton 1984).

CATEGORY	TAXA	AVERAGE ANNUAL HARVEST	
		No. Animals	Biomass, kg
HERBIVORES	Nutria	3,548	19,869*
	Muskrat	1,432**	1,293***
	American Beaver	111	1,254***
Subtotal			22,416
PREDATORS	Raccoon	486	2,333
	Canadian River Otter	6	51
Subtotal			2,384
TOTAL			24,800

* Based on average adult biomass of 5.6 kg.

** Excluding Pacific County harvest

*** Based on average muskrat (kits, subadults and adults of both sexes) biomass of 0.9 kg.

**** Based on average beaver biomass of 11.3 kg.

Deposit Feeders. In general, all deposit-feeder populations in the estuarine ecosystem are assumed to be indigenous because of their limited motility as reproductive units. Net export of deposit-feeding epibenthic zooplankton out of the estuary may occur via bedload transport processes, but their flux cannot be estimated. Few, if any, deposit-feeding organisms occur in the river above the estuary, although the distribution of the exotic clam Corbicula manilensis may extend into true fluvial habitats. Thus, import of deposit-feeders from riverine discharge is either negligible or inestimable.

Suspension Feeders. Pelagic zooplankton data (Jones and Bottom 1984) could not be used to measure the fluvial import of freshwater zooplankton from the river above the estuary because the most upriver station was positioned approximately at the downriver limit of the tidal-fluvial zone, well below the upriver boundary of the estuary proper. An indication of the potential import of freshwater zooplankters can, however, be derived from Craddock et al.'s (1976) 13-month plankton sampling in the river near Prescott, Oregon, in 1968-1969. Their samples, which were obtained with daylight vertical hauls of a 0.5-m Nansen net or a 127-mm Clarke-Bumpus (both with 0.150-mm mesh) to varying depths as deep as 15 m, indicated that cladocerans (Daphnia and Bosmina) and cyclopoid copepods were the principal plankters imported into the estuary. Maximum densities as high as about 4000 m^{-3} were reported during August and September. These density estimates were extrapolated by the mean monthly 1980-1981 discharge rates under the assumptions of conservative mixing of a temporally [monthly] constant source and linear decline in zooplankton density between November and March (when Craddock et al. 1976 did not sample). The resulting estimates of monthly and annual import of freshwater pelagic zooplankton into the estuary in 1980-1981 (Table 7.56) indicated that import ranged between 0.6 x 10^{12} m^{-3} mo^{-1} during March to 38.8 to 41.1 x 10^{12} m^{-3} mo^{-1} during the high flow and early portion of the low flow seasons. Assuming 0.01 mg average wet weight $zooplankter^{-1}$ and an average 5% carbon content, similar estimates of freshwater zooplankton biomass range between 281 and 20,528 kgC mo^{-1}, for a total annual import of approximately 102 MT C yr^{-1}.

It is more difficult to estimate the average export of pelagic zooplankton from the estuary to the Pacific Ocean because, given the vertically-integrated sampling design during the zooplankton studies (Jones and Bottom 1984), there is no discrete estimate of densities of euhaline (marine) zooplankters entering from outside the estuary.

Predators. Motile macroinvertebrates can be assumed to move into and out of the estuary at the entrance but import rates cannot be estimated from any existing information, including the data generated during these studies.

Marine mammals present the most extreme case of import and export, especially if the extent of their migrations is considered. Unlike the more ephemeral, nektonic predators such as pelagic fishes, however, sea lion and seal movements are comparatively predictable. Coincident with the dispersal of males after the May-June breeding season in Mexico and California, adult and subadult California sea lions move northward to

Table 7.56. Estimated monthly import of freshwater pelagic zooplankton to Columbia River Estuary, 1980–1981, based upon 1968–1969 plankton sampling near Prescott, Oregon (RM-71) (Craddock et al. 1976).

	APPROXIMATE MONTHLY DISCHARGE RATE (m^3s-1)		ZOOPLANKTON DENSITY (no. m^{-3})	ESTIMATED MONTHLY ZOOPLANKTON IMPORT	
MONTH	1968–1969	1980–1981	1968–1969	ABUNDANCE (no.x10^{12})**	BIOMASS (kgC)***
JANUARY	9,572	8,553	476*	12.20	6,102
FEBRUARY	7,646	8,892	253*	4.68	2,340
MARCH	6,768	6,344	31	0.56	281
APRIL	11,356	6,358	87	1.53	763
MAY	13,112	8,170	190	6.67	3,336
JUNE	10,790	10,719	1,468	41.06	20,528
JULY	7,689	6,188	1,907	39.27	19,637
AUGUST	4,234	2,560	3,421	38.80	19,398
SEPTEMBER	3,752	3,781	2,975	28.93	14,466
OCTOBER	3,257	3,653	934	8.15	4,074
NOVEMBER	5,650	5,437	922	13.50	6,751
DECEMBER	8,836	9,629	699*	16.54	8,271
ANNUAL TOTAL BIOMASS (kgC)					101,873

* Estimated as linear decline between November and March

** 1980–1981 densities estimated by adjusted (assuming conservative dilution) density from 1968–1969 x 1980–1981 discharge rate x 86,400 x days in month

*** Assuming 0.01 mg average wet weight per organism x 5% C content overwinter along the coast of Oregon, Washington, and British Columbia (Mate 1975). Only males appear to utilize the Columbia River Estuary, arriving initially in September and emigrating by late June (Jeffries et al. 1984). Their population reaches a spring maximum at the South Jetty (Figure 7.52) but many animals move through the estuary, as far upriver as Bonneville Dam, in apparent response to the availability of principal prey resources such as eulachon.

Similar to the California sea lion population, the northern sea lion population utilizing the Columbia River estuary is highly migratory. Northern sea lions appear in the estuary in October after the breeding season, maintain their abundance through the winter, and emigrate from the estuary by mid-July (Jeffries et al. 1984). Unlike the California sea lion, however, adults and subadults of both sexes were present in the estuarine population and their distribution was restricted to the estuary below Tongue Point.

Although harbor seals do not undergo the extensive reproductively-related migrations of sea lions, the amount of interchange among coastal areas along the Pacific Northwest coast is considerable. The addition of data from radiotagged and marked seals from the Columbia River Estuary to information from earlier studies indicates that these seals move actively between the estuaries at Grays Harbor, Washington (35 km north) and Tillamook Bay, Oregon (25 km south) in response to seasonal prey abundance and availability of preferred pupping areas in Tillamook Bay (Figure 7.66; Jeffries et al. 1984).

Thus, import and export of sea lion and seal population biomass to and from the estuary is both spatially and seasonally dynamic. In the case of sea lions, there is some predictable nature to the temporal pattern but movement within the estuary is relatively random, depending upon the distribution and abundance of prey assemblages. In contrast, seal populations maintain some fidelity to specific haulout sites within the estuary (Table 7.57) but the flux of animals in and out of the estuary is considerable. Of the (58) individual seals radiotagged inside the Columbia River Estuary, 75% (43) were found at haulout sites outside the estuary (Jeffries et al. 1984). In some cases, movement into and out of the estuary between haulout sites occurred in as little as 12 hr between consecutive low tide cycles.

Fecal Discharge-Consumption

As mentioned earlier, organic carbon can be recycled through the Consumption process by reingestion of fecal matter, principally by deposit-feeders but also by suspension-feeders if the fecal particles fit the selection criteria of these organisms. However, although a potentially important route of internal cycling of organic matter in the estuary, it was not measured for any organism.

Natural Mortality

Non-consumption related natural mortality was not measured directly during any of the CREDDP investigations of consumer populations in the estuary. In fact, natural mortality other than via predation may not be

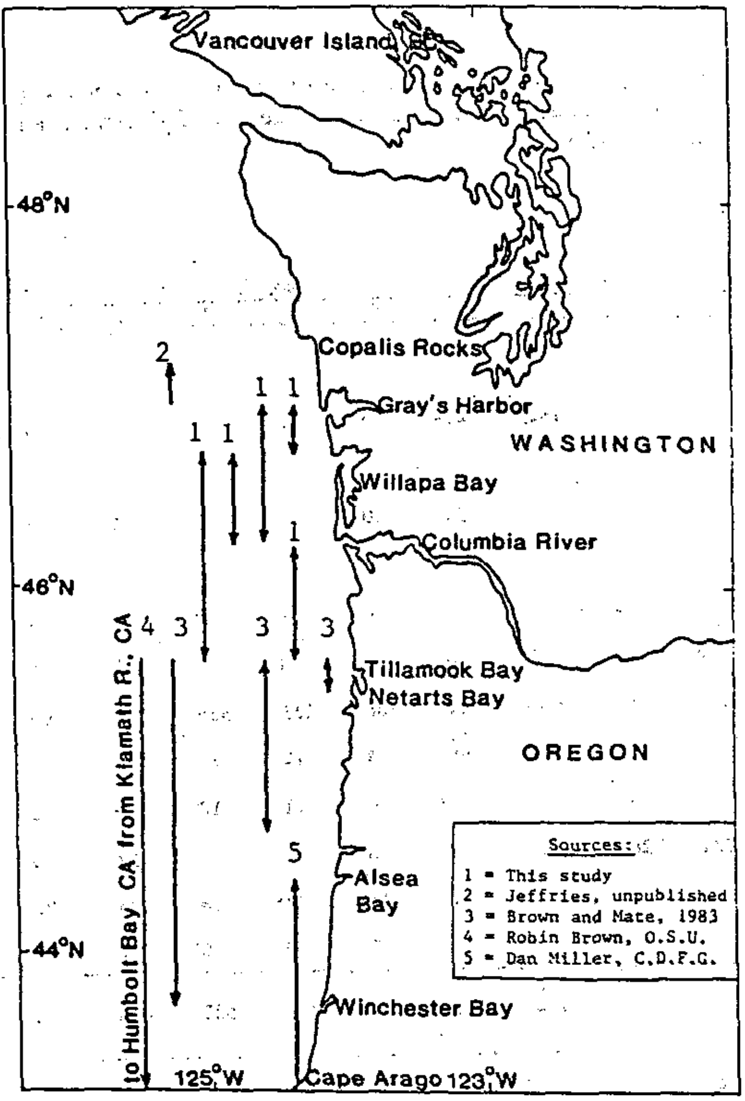


Figure 7.66. Movement and interchange patterns of harbor seals along the Washington and Oregon coasts (Jeffries et al. 1984).

Table 7.57. Maximum monthly haulout counts of pinnipeds from low tide aerial surveys (except as noted), Columbia River Estuary, 1980 - 1983.

SPECIES	MONTH											
Haulout Location	J	F	M	A	M	J	J	A	S	O	N	D
CALIFORNIA SEA LIONS												
South Jetty	75	100*	181	145*	75	20	0	0	5	42	NS**	21
NORTHERN SEA LIONS												
South Jetty	61	50	19	32	40	5	2	1	6	5	NS	52
HARBOR SEALS												
South Jetty	0	0	1	0	0	1	0	3	4	0	NS	0
Baker Bay	0	NS	0	20*	1	0	0	7	11	25*	NS	0
Desdemona Sands	566	NS	650*	884	568	273	525	378	563	223	230*	301
Taylor Sands	444	NS	548	260	4	22	21	0	7	59	NS	174
Grays Bay	1	NS	0	20*	4	11	10	0	12	0	NS	0
Miller Sands	381	200*	82	137	0	1	0	32	0	6	NS	46
Green Island	0	NS	0	0	16	26*	38	35	26	0	NS	0
N. of Woody Is.	72	55*	3	18	0	0	0	0	0	0	NS	0
COLUMBIA RIVER ESTUARY	1422	255*	898	1182	568	273	525	405	595	301	230*	521

* Visual estimate from airplane, boat or jetty
** NS = Not Surveyed

a common factor affecting most consumer populations. Some terrestrial and wetland mammals may be the exception, however. Under no or low predation pressure, some mammal populations appear to be experiencing density-dependent disease epidemics and parasite infestations. One of the few estimates of non-consumption natural mortality is Davison's (1979) statement that abomasal nematodes (Osteragia sp.) and stomach worm (Haemonchus sp.) infestations contributed to the death of three to eight Columbian white-tailed and Columbian black-tailed deer. Necrobaccillosis ("foot rot"), bacterial infections, and malnutrition stress are also suggested to produce some unknown natural mortality (Merker and Fenton 1984).

Natural mortality may also occur as catastrophic, atmospheric-driven events such as result from floods and storms which, in extremes, could bury or dislodge less-mobile organisms such as benthic infauna.

Life History Changes in State

By definition, transformations and transfer of state variables into and out of the Consumption Processes subsystem associated with life history changes in state do not occur because, but for a few exceptions, all life history forms are consumers. The exceptions involve fish and invertebrate eggs which have internal energy sources (e.g., yolk) for short periods of their early life history. On the other hand, such transfers occur internally among consumer subsystems.

Internal Changes of State

Consumption

Under some circumstances, living organic matter produced by consumer organisms (as opposed to fecal and DOC production or natural mortality contributions to the detritus resource) can constitute a food resource internal to the Consumption Process. For example, reproductive products such as eggs and larvae released within one consumer subsystem (e.g., infaunal bivalve in Suspension-feeding subsystem) are consumed both within that subsystem (e.g., by the same and other suspension-feeding bivalves) and by organisms in other consumer subsystems (e.g., larval fish in the Predation subsystem). This transfer of living material within the overall Consumption Process was not measured directly but it is assumed to be accounted for in several indirect measurements and calculations. Specifically, the biomass of larvae consumed by suspension-feeding consumers is an unknown proportion of the non-chlorophyllous organic matter estimated in Section 7.2.5.

Life History Changes in State

Life history changes in state constitute an important, but again inestimable, flux of living organic matter between Consumption Process subsystems but which does not involve consumption *per se*. Instead, this represents a direct, ontogenetic transformation of consumer biomass from one subsystem to another. The prevalent direction of this transformation is between benthic (e.g., benthic infauna, epibenthic zooplankton, motile macroinvertebrates) and pelagic (e.g., pelagic zooplankton and fishes) subsystems (see Figures 6.9 and 6.10) through the production of planktonic, suspension-feeding larvae and juveniles by both deposit-feeding and suspension-feeding adults (thus, the inter- and intrasubsystem transformations). Ultimately, a small proportion (due primarily to predation losses, somewhat less to non-predation natural mortality and export) of these planktonic consumers will metamorphose and recruit back to the benthic environs and assume their adult feeding mode.

Although many of the planktonic larval and juvenile stages of benthic and epibenthic consumers were assessed during the pelagic zooplankton studies in the estuary (Jones and Bottom 1984), the actual rates and magnitudes of the transformations between the benthos and water column cannot be determined from this and the corresponding (benthic infauna, epibenthic organisms) CREDDP investigations.

7.4 SUMMARY

Based upon the previous descriptions organized around the conceptual process model, the dynamics of primary food and consumption proccesses in the Columbia River Estuary can be summarized. While the quantitative estimates of state variables and process rates principally reflect the results of specific CREDDP measurements during 1980 and 1981, the functional relationships and process dynamics illustrated by these results are assumed to be more broadly descriptive of the structure and dynamics of the Columbia River estuarine ecosystem.

7.4.1 Primary Production

Water Column

The estuary is dominated (over 75%) by freshwater diatoms, including both planktonic and benthic taxa. Circulation dynamics were responsible for differing taxa composition in different regions of the estuary: almost no freshwater diatoms were found in Baker Bay; Clatsop Spit phytoplankton contained some freshwater taxa; and, Youngs Bay had a mixture of freshwater and estuarine benthic and planktonic diatom taxa. These distributions illustrated the extent of the distribution of freshwater diatoms through the estuary and of export to the ocean.

Phytoplankton taxa composition, standing crop, and productivity were affected greatly at the boundary between freshwater and seawater (0 to 5 ppt salinity) in the estuary. Live cells are more abundant, and standing crop and production higher, in the freshwater region as compared to the more saline region immediately downriver. Evidence suggests that live, chlorophyll-containing cells are lysed and converted to dead, non-chlorophyllous detrital particles at this freshwater-seawater interface. The mass of total particulate carbon does not change through the estuary, however.

Without considering the effect of the Mount St. Helens eruption in May 1980 (which apparently shifted peak phytoplankton standing stock and production from spring to mid-summer), import and export of phytoplankton-derived carbon was estimated to be 5.6 x 10^4 MT C yr^{-1} and 3.4

$\times 10^4$ MT C yr^{-1}, respectively, with an estimated loss (by difference) of 2.2×10^4 MT C yr^{-1} within the estuary.

From July through February, over 70% of the total loss of living phytoplankton carbon was accounted for by unevaluated losses due to death and sinking, nighttime respiration, excretion, unevaluated grazing, etc. Only during periods of high river discharge did export of phytoplankton carbon exceed unevaluated losses in the estuary.

The annual production of phytoplankton carbon within the estuary was estimated to be 1.7×10^4 MT C yr^{-1}, or 68 gC m^{-2} yr^{-1}. Import of phytoplankton carbon from upriver always exceeded primary production within the estuary, although the two inputs were about equal during the low flow season. On an annual basis, 75% of the phytoplankton carbon was supplied from upriver, with only 25% produced <u>in situ</u> within the estuary.

Light appears to be the major factor limiting phytoplankton primary production in the estuary. Both intensity of solar radiation and attenuation of light within the water column are critical variables affecting the rates of primary production per unit of phytoplankton biomass or per unit of phytoplankton chlorophyll <u>a</u>. Of the major inorganic nutrients necessary for phytoplankton growth, only nitrogen appears to become depleted to the point of limiting phytoplankton growth and production.

Benthic Algae

Microalgae are the most abundant group of benthic plants associated with the tidal flats of the estuary. Assemblages of microalgae on the tidal flats consist almost entirely of diatoms, while blue-green algae are occasionally found growing on the sediment beneath emergent vascular plants in the low marsh. The only species of macroalgae observed on the tidal flats during the study was <u>Enteromorpha intestinalis</u>. This filamentous green alga was abundant in sediment samples from the low marsh in April and May at a site in Youngs Bay and also occurred in association with individual shoots of eelgrass on a tidal flat in Baker Bay.

A detailed quantitative analysis of the taxonomic structure of the benthic diatom flora indicated that the taxa composition in Cathlamet Bay, Grays Bay, and the Upper Estuary region above Cathlamet Bay are similar. The Youngs Bay benthic diatom flora was more similar to the floras of these upriver regions than to the flora of Baker Bay, a pattern apparently related to freshwater input into Youngs Bay from the Lewis and Clark River, the Youngs River, and the Columbia River itself. Using the taxa composition of the diatom flora as a salinity indicator, a statistical analysis indicated that Cathlamet Bay, Grays Bay, and the Upper Estuary regions are freshwater regions in tidal flat habitats, while the tidal flats in Baker Bay are under the influence of brackish water. Youngs Bay apparently is influenced to some degree by slightly brackish water, although intermittent periods of high freshwater discharge are responsible for the presence of a large number of freshwater planktonic and benthic diatom taxa in the sediment-associated flora.

Mean biomass of benthic microalgae at five intensive study sites were 1.38 ug chl *a* cm^{-3} at Clatsop Spit, 26.44 ug chl *a* cm^{-3} at Youngs Bay, 25.06 ug chl *a* cm^{-3} at Baker Bay, 10.33 ug chl *a* cm^{-3} at Grays Bay, and 9.02 ug chl *a* cm^{-3} at Quinns Island; corresponding mean rates of benthic gross primary production at the intensive study sites were 5.22, 84.22, 42.50, 33.01, and 29.56 mgC m^{-2} hr^{-1}. In general, there was relatively little seasonal change in the microalgal biomass at these sites, and the biomass was usually highest in the low marsh and lowest close to the river channel. Production rates were highest from March through October and lowest during winter months. Low marsh and upper tidal flat habitats tended to have the highest production rates and lower tidal flat habitats the lowest rates.

Sediment-associated assemblages of benthic microalgae appeared to reach their maximum light-saturated rate of photosynthesis at light intensities of between 200 and 400 uE m^{-2} sec^{-1}, or between 10% and 20% of the intensity of full sunlight. Experiments indicated that a 10°C short-term increase in temperature within the tolerance range will double the hourly rate of production. In addition to water column turbidity and daylength, sediment properties and stability were considered to be the principal factors controlling benthic primary production. Although the effects of deposit feeding, direct grazing on benthic microalgae, or bioturbation by benthic and epibenthic organisms were not evaluated, animal activity was not conspicuous and may be minor in the Columbia River Estuary compared to other coastal and inland estuaries in the region.

Estimated annual gross primary production for the intensive study sites at Clatsop Spit, Youngs Bay, Baker Bay, Grays Bay, and Quinns Island were 8.04, 120.94, 69.25, 44.56, and 33.46 gC m^{-2} yr^{-1}, respectively. From these data and the annual rates calculated for other (survey) sites, it was estimated that the total annual benthic gross primary production for the tidal flat habitats of the estuary is approximately 1.5 x 10^3 MT C yr^{-1}, with the flats in the downriver regions of the estuary being more productive than those in the freshwater regions upriver.

Vascular Plants

Submergent vascular plants in tidal flat habitats are rare and their distribution extremely patchy. Eelgrass (*Zostera marina*) has a sparse distribution in Baker Bay and has been collected in Trestle Bay, but the estuary apparently lacks the habitat necessary to support the large, dense eelgrass beds that are found in other coastal estuaries of the region. Possible factors limiting the growth of eelgrass in the Columbia River Estuary include low salinity regimes, high turbidities, and the properties or instability of the sediment. Other submergent vascular plants can be found at freshwater sites in Grays Bay.

Emergent vascular plants are prominent primary producers on 5,873 ha in the estuary, 3,341 ha of which are marsh habitats dominated by herbaceous plants and 2,531 ha are swamp habitats dominated by woody plants. Using a numerical classification analysis, six emergent plant assemblages were discriminated: (1) low marsh habitats in brackish water dominated by *Carex lyngbyei*; (2) high marsh habitats in the estuary's estuarine mixing zone characterized by *Oenanthe sarmentosa*, *Lotus corniculatus*, *Mimulus guttatus*, *Carex lyngbyei*, and *Deschampsia caespitosa*; (3) low marsh *Carex lyngbyei* habitats in the estuarine mixing zone; (4) *Typha latifolia* marsh in the upriver region of the tidal-fluvial zone; (5) a low marsh habitat near Tongue Point dominated by *Myosotis laxa* and *Equisetum* sp.; and (6) a unique marsh habitat in Trestle Bay which included primarily *Lathyrus palustris*, *Potentilla pacifica*, *Carex lyngbyei*, *Juncus balticus*, and *Agrostris alba*.

On an areal basis, the aboveground standing crop of emergent vascular plants averaged 214 gC m^{-2} yr^{-1}, compared to 692 gC m^{-2} yr^{-1} of belowground standing crop. The estimated mean net annual aboveground production was estimated to be 386 gC m^{-2} yr^{-1}, of which an estimated 58 gC m^{-2} yr^{-1} (15%) was lost to herbivorous consumers and 40 gC m^{-2} yr^{-1} (10%) by leaching of dissolved organic matter; minimum export of detritus from aboveground production out of swamp and marsh habitats was estimated to be 184 gC m^{-2} yr^{-1}. Of the aboveground production, 148 gC m^{-2} yr^{-1} (38%) was estimated to be translocated to belowground roots during the fall season.

7.4.2 Detritus Production

Excluding the effect of the fluvial detritus load generated by the eruption of Mount St. Helens in May 1980, annual import of particulate detrital carbon into the estuary was estimated from measurements of non-chlorophyllous POC to be 14.6 x 10^4 MT C yr^{-1}. Export was estimated to be 15.9 x 10^4 MT C yr^{-1}. Transformation of phytoplankton to detritus within the estuary was estimated to account for 3.9 x 10^4 MT C yr^{-1}; using a 47% conversion factor, it was estimated that 5.3 x 10^3 MT C yr^{-1} of marsh vascular plant carbon becomes detritus. Assuming that most of the benthic primary production is consumed directly rather than being converted to detritus, a total of 19.1 x 10^4 MT C yr^{-1} of detrital particulate carbon enters the estuarine detrital pool. Given the 15.9 x 10^4 MT C yr^{-1} exported from the estuary to the plume and ocean zone, an estimated 3.2 x 10^4 MT C yr^{-1} is lost (consumed or enters a detrital "sink") within the estuary.

7.4.3 Consumption

Wetland Herbivory

Prominent wetland herbivores in the estuary include avifauna (mallard and American widgeon ducks, black-capped chickadee), terrestrial mammals (Columbian white-tailed and black-tailed deer, deer mouse, Townsend's vole), and aquatic mammals (nutria, muskrat, American beaver). Herbivore activity is concentrated in the marsh and swamp habitats located in the peripheral bays and in the islands of the Cathlamet Bay and Fluvial Regions.

Given density estimates between 0.02 individuals ha^{-1} (Columbian white-tailed deer) and 20.8 ha^{-1} (nutria), it was estimated that between 745 and 780 MT C of wetland herbivores occupy the estuary. The three principal wetland herbivores (muskrat, nutria, beaver) were estimated to consume between 372 and 3,017 MT C yr^{-1} but an unkown proportion of the estimated consumption by terrestrial herbivores (8 to 11 MT C yr^{-1} for deer) and the lack of data for avian and small mammal herbivores suggests that macroherbivory in the estuary is considerably underestimated.

Thus, herbivory by mammals and avifauna accounts for between 380 and 3,028 MT C yr^{-1} transferred to the primary consumer level of the estuarine food web. However, herbivory by insects is completely unassessed.

Deposit Feeding

Benthic infauna (bivalves, oligochaetes, polychaetes, gammarid amphipods) and epibenthic zooplankton (harpacticoid, calanoid, and cyclopoid copepods, and gammarid amphipods) comprised the principal deposit-feeding organisms in the estuary. Reciprocal averaging ordination of the deposit-feeding benthic infauna density data defined four groups, including taxa assemblages (1) uniquely associated with tidal-fluvial zone habitats; (2) prevalent in protected tidal flat habitats in both the plume and ocean and estuarine mixing zones; (3) channel bottoms and exposed tidal flats in the estuarine mixing zone; and (4) exposed tidal flats and channel bottoms in the plume and ocean and estuarine mixing zones. These groups were distinguished principally by: (1) Corophium salmonis, Heleidae, Chironomidae, and Oligochaeta; (2) Hobsonia florida, Macoma balthica, and Neanthes limnicola; (3) Eohaustorius estuarius, Neanthes limnicola, and Rhynchocoela; and (4) Rhynchocoela and Paraphoxus milleri, respectively.

The standing crop of benthic infauna was closely related to sediment structure, and in particular the fraction of fine particles and the percent organic content. As a result, the peripheral bays in the downriver regions of the estuary sustain higher standing crops (as high as 3,487 mgC m^{-2} in Baker and Trestle Bays) than protected tidal flats in other regions of the estuary (411 and 456 mgC m^{-2} in Grays Bay and Quinns Island tidal flats, respectively). The lowest standing crop values were found in the high-energy, course-grained habitats of all channel bottoms (46 to 61 mgC m^{-2}) and demersal slopes (28 mgC m^{-2} in the Mid-Estuary Shoals region) in the estuarine mixing zone. Production of deposit feeding benthic infauna was estimated to total 356.3 MT C yr^{-1}, second only to suspension feeding zooplankton though only 11% of the total production by estuarine consumers. Backcalculating from this production estimate, it was estimated that 1,943.3 MT C yr^{-1} is consumed by deposit feeding infauna.

At least half of the standing stock of epibenthic zooplankton in the estuary were considered to be deposit feeders, and in particular the harpacticoid copepods (predominantly Scottolana canadensis, Microarthridion littorale, Tachidius triangularis, Atheyella sp.). The deposit feeding gammarid amphipod Corophium salmonis, which is very prominent in the benthic infauna assemblages because of its tubericolus life style, was also a prominent member of the epibenthic zooplankton assemblage when male amphipods emerged from the sediment. Numerical classification analysis (clustering) indicated that epibenthic assemblages change dramatically with hydrologic season. During both high and fluctuating flow seasons, there is comparably discrete separation of fluvial taxa (e.g., the harpacticoids Tachidius, Attheyella, the ostracod, Limnocythere sp, and Corophium) from more euryhaline taxa (e.g., the harpacticoids Scottolana canadensis, Ectinosomidae, Microarthridion and Bryocamptus). During the decreased stratification, increased mixing and salinity intrusion of the low flow season, however, the structure of the epibenthic zooplankton assemblages becomes much more complex, with fluvial, euryhaline, and euhaline taxa included within several of the assemblages spread throughout the estuary.

Densities of deposit feeding epibenthic zooplankton were estimated to range widely between about 43 and about 20,000 individuals m^{-2} and standing crop values between 0.9 and about 1,932 mg m^{-2}. Average standing stock was highest (about 10,905 m^{-2}) in tidal flat habitats and lowest (about 5,000 m^{-2}) in channel bottom habitats. Maximum standing stock consistently occurred within the estuarine mixing zone, but shifted farther upriver between the high and low flow seasons in conjunction with the increased salinity intrusion and location of the turbidity maximum. Based on the estimated total annual production of 32.36 MT C yr^{-1}, consumption by deposit feeding epibenthic zooplankton was estimated to be 161.8 MT C yr^{-1}.

Therefore, the combined annual consumption rate of deposit feeders is approximately 2,105 MT C yr^{-1}.

Suspension Feeding

Suspension-feeding benthic infauna were limited primarily to two bivalves, Corbicula manilensis, which was distributed exclusively within the tidal-fluvial zone, and Mya arenaria, which occurred in tidal flat and minor channel habitats in the plume and ocean zone and downriver portions of the estuarine mixing zone. Mya dominated the standing stock distribution, which peaked at 77 mgC m^{-2} in the Baker and Trestle Bays tidal flats. Total annual consumption by suspension feeding benthic infauna was estimated to be about 170 MT C yr^{-1}.

Most of the suspension-feeding epibenthic zooplankton found in the estuary are calanoid and cyclopoid copepods and cladocerans, the most prominent of which is the endemic calanoid, Eurytemora affinis. In contrast, the other cyclopoids and cladocerans are pelagic, freshwater taxa which, especially in the vicinity of the turbidity maximum, have been concentrated in the benthic boundary layer. Eurytemora dominated standing stock during the high flow season, when the population was concentrated in the downriver reaches of the estuarine mixing zone by the high freshwater discharge; during the low flow season, however, the population's distribution expanded diffusely throughout the estuarine mixing zone and appeared concentrated only within the turbidity maximum. Annual consumption by the suspension feeding component of the epibenthic zooplankton was considered to be approximately equal to that of the deposit-feeders, about 167 MT C yr^{-1}.

Suspension-feeding pelagic zooplankton of channel water column habitats fall into three assemblages, distributed along the longitudinal salinity gradient according to seasonal variations in river discharge: (1) a dominantly freshwater group of cladocerans (e.g., *Daphnia* spp., *Bosmina longirostris*); (2) endemic estuarine calanoid copepods (*Eurytemora affinis*); and (3) a polyhaline group of calanoid (e.g., *Pseudocalanus elongatus*, *Paracalanus parvus*, *Calanus pacificus*, *Acartia clausi*, *A. longiremis*, *Centropages abdominalis*) and cyclopoid (e.g., *Corycaeus anglicus*) copepods characteristic of the plume and oceanic water masses intruding at the mouth of the estuary. Compared to the high flow periods during the winter and spring, during the low flow season the plume and ocean zone assemblage is more complex and widely distributed and the freshwater taxa are more widely mixed with the estuarine and plume and ocean assemblages. Despite the high energy state during the high flow season, average density of suspension-feeding pelagic zooplankton in the estuary were generally at a maximum during this season, particularly in the estuarine assemblage (about 2,300 individuals m^{-2}), reflecting a close correspondence with phytoplankton (and possibly detritus) food resources. The estimated annual production rate of pelagic zooplankton, 2,505 MT C yr^{-1}, was the highest of any animal groups in the estuary; this would suggest an average annual consumption rate of 1.3×10^{4} MT C yr^{-1}.

Combined, suspension-feeding accounts for the consumption of approximately 13,337 MT C yr^{-1} of phytoplankton and detrital carbon within the estuary.

Predation

Errantate polychaetes (e.g., *Eteone* sp., *Nephtys californiensis*) and amphipods (*Eogammarus confervicolus*) constituted the benthic infauna predators. Maximum standing crop of predatory polychaetes (10 to 100 mgC m^{-2}) occurred in protected tidal flat habitats in the tidal-fluvial zone, while amphipod standing crop varied between 0.1 and 10 mgC m^{-2} throughout the estuarine mixing and tidal-fluvial zones. Mean standing crop of all benthic infauna predators was generally an order of magnitude higher (144 to 800 mgC m^{-2}) in the Cathlamet Bay and Fluvial Regions compared to more estuarine or marine regions downriver (0 to 25 mgC m^{-2}). As a result of their high standing stock and turnover rate, these infaunal predators illustrated the highest production rate (61.2 MT C yr^{-1}) of any predator group. This high level of production implied a corresponding annual consumption rate of about 300 MT C yr^{-1}.

Motile macroinvertebrates (Dungeness crab, *Cancer magister*, and the crangonid shrimp, *Crangon franciscorum*) and certain zooplankters (mysids) were prominent predators in the plume and ocean and estuarine mixing zones. Although Dungeness crab, *Cancer magister*, are voracious carnivores on benthic infaunal and epifaunal macroinvertebrates, their distribution is relatively restricted to the channel bottom habitats in the plume and ocean zone and lower reaches of the estuarine mixing zone within about 10 km of the mouth of the estuary; maximum densities were typically less than 0.05 individuals m^{-2} during the high flow season but may occur as high as 0.2 m^{-2}. Crangonid shrimp and mysids, on the other hand, were shown to be important predators on epibenthic zooplankton (particularly *Scottolana canadensis*) throughout the plume and ocean (primarily the stenohaline-marine mysid, *Archaeomysis grebnitzkii*) and estuarine mixing (primarily *Neomysis mercedis* and *Crangon franciscorum*) zones. Their seasonal spatial and standing stock distributions are highly associated with their epibenthic prey resources, the extent of salinity intrusion, and the location of the turbidity maximum. Overall, this assemblage of predatory macroinvertebrates accounts for about 27 MT C yr^{-1} annual production, approximately equal to the production rate of fish in the estuary and indicative of an annual consumption rate of about 135 MT C yr^{-1}.

Although not a diverse assemblage, larval fish (only eleven taxa, of which only *Cottus asper* and general osmerids are abundant) occurred in high densities (100 to 300 individuals m^{-2}) immediately prior to the low flow season. As a result of their high foraging rate during this short period, the estimated production (44.4 MT C yr^{-1}) of larval fish ranked higher than that of juvenile and adult fishes and implied an equally high annual consumption rate of about 220 MT C yr^{-1}.

Of the 75 species of fish documented in the estuary, 42 were represented by less than 10 individuals and only 18 were considered of economic or ecological importance. The ten "key" species included American shad, Pacific herring, northern anchovy, coho salmon, chinook salmon, longfin smelt, shiner perch, Pacific staghorn sculpin, English sole, and starry flounder, all of which occurred predominantly as juveniles (subyearlings and early yearlings) rather than as adults. Despite considerable seasonal variation in fish taxa-life history stage occurrence and standing stock, ten to twelve fish assemblages were consistently distributed among the three zones of the estuary. Among the major factors influencing the composition and distribution of fish assemblages are: (1) seasonal cycles in migration and life history of the fishes; (2) longitudinal salinity gradient as influenced by seasonal variation in riverine discharge of freshwater and neap-spring tidal cycles; (3) the distribution of four habitats (protected embayments, pelagic channels, demersal channels, demersal slopes) within the three zones; and (4) density and distribution of preferred invertebrate prey taxa.

Water column (pelagic) fishes occurred in densities as high as 0.3 individuals m^{-2} and standing crops as high as 3.6 g m^{-2}, with the highest standing stock occurring at the mouth of the estuary. Demersal slope assemblages occurred at approximately the same standing stock level, as high as 0.3 individuals m^{-2} and 4.3 g m^{-2}, respectively; highest density occurred in the region of Youngs Bay, while the highest standing crop occurred in the region of Cathlamet Bay. The highest standing stock was typically illustrated by channel bottom fish assemblages, averaging 1.0 individuals m^{-2} and 11.7 g m^{-2}. Although sampled separately and less frequently, there were indications that tidal flats in the peripheral bays and on the mid-estuary shoals supported densities and standing crops as high as 2.3 m^{-2} and 34.5 g m^{-2}, respectively. Feeding rates also varied among fish assemblages and estuarine zones, with the highest rates indicated by channel bottom assemblages and average rates in all assemblages occurring in the estuarine mixing zone. Average annual consumption was estimated to be approximately 1,086 MT C yr^{-1}.

Four assemblages of carnivorous birds (western grebe, double-crested cormorant, hybrid gulls, and a multi-species shorebird assemblage) were seasonally (typically winter-spring) common and abundant in the estuary. Distributions through the estuary reflected feeding, nesting, and loafing activities. The tidal flats, marshes, and minor channels associated with peripheral bays were the habitats supporting most of the foraging activities by these birds. Indirect estimation of annual consumption by predatory birds suggests that it is relatively low, i.e., on the order of 0.3 to 0.6 MT C yr^{-1}.

Three terrestrial-wetland predators are important in the estuary, the Canadian river otter, raccoon, and vagrant shrew. Although there was not enough data to assess the standing stock and trophic role of vagrant shrews, they were locally abundant in several habitats and may play a major role as a prominent insectivore in the estuarine food web. The Canadian river otter and raccoon were shown to be abundant in the swamp and high marsh habitats adjacent to the peripheral bays and among the islands of Cathlamet Bay. Average raccoon density and standing crop were estimated to be 0.08 individual ha^{-1} and 0.32 kg wet weight ha^{-1}, respectively, and Canadian river otter, 0.02 ha^{-1} and 0.17 kg wet weight ha^{-1}. Consumption of crayfish, <u>Corbicula manilensis</u>, birds, Rosaceae fruit, and sculpins by raccoon was estimated to be 8.52 MT C yr^{-1}; consumption of crayfish, sculpins, carp, unidentified fish, and starry flounder by Canadian river otter was estimated to be between 1.37 and 1.63 MT C yr^{-1}.

Four marine mammals (northern sea lion, California sea lion, harbor seal, northern elephant seal) are common to the estuary, although the elephant seal is not extremely abundant. Sea lions are winter residents concentrated (about 200 individuals) at the mouth of the estuary, while between 100 and 800 harbor seals occupy essentially all regions of the estuary year-round. However, movement and interchange of harbor seals among Tillamook Bay, the Columbia River Estuary, Willapa Bay, and Grays Harbor is extensive and suggests response to seasonal prey abundance and availability of preferred pupping areas. Overall, total marine mammal densities ranged from 1.25 individuals km^{-2} during the low flow season to a maximum of 3.55 individuals km^{-2} in the high flow season; standing crop ranged from 105.53 kg wet weight km^{-2} during the low flow season to 347.87 kg wet weight km^{-2} during the high flow season. Motile macroinvertebrates (Dungeness crab, crangonid shrimp), bivalves, and fish (including predominantly longfin smelt, Pacific staghorn sculpin, Pacific tomcod, English sole, starry flounder, snake prickleback, Pacific herring) comprised the prey resource of sea lions and seal in the estuary. Indirect estimates of total annual consumption by sea lions in the estuary was 69.55 MT C yr^{-1} and by harbor seals was 244.21 MT C yr^{-1}, for a total of 313.76 MT C yr^{-1} for all marine mammals.

Thus, total consumption by these secondary and tertiary level carnivores annually equals approximately 2,057 MT C yr^{-1}.

8. ECOSYSTEM ANALYSES BY REGIONS AND HABITAT TYPES

8.1 ESTUARINE REGIONS

The eight major regions used to divide the Columbia River estuary (Figure 7.1) were delineated principally on the bases of temperature-salinity characteristics of the water, tidal energy, and sediment grain size and sorting (see Chapters 3 and 4). Seasonal considerations and spring-neap tidal cycles prevented rigid demarcation of regions, particularly in mid-estuary; nevertheless, even with the time-dependent nature of the physical phenomena, reasonably coherent boundaries could be defined and used for examining physical and biological processes in the estuary.

Three water masses with distinct temperature and salinity characteristics are mixed within the estuary (see Chapter 2). River Water (RW) has zero salinity and a temperature that varies greatly with season. Surface Ocean Water (SOW) is the warmest water type with near-oceanic salinities (10-14°C temperatures and 31.5-32.5$^{\circ}/_{\circ\circ}$ salinities, depending on the season). Sub-Surface Ocean Water (SSOW) is the densest water type, with 7.5-8.0°C temperatures and 33.4-33.8$^{\circ}/_{\circ\circ}$ salinities. Estuarine Water (EW) was defined as the intermediate water mass formed within the estuary, resulting from any mixture of RW, SOW, and SSOW; the characteristics of EW are highly variable. Most of the water in the Columbia River estuary is a mix of only two of the end-member water types, SOW and RW. Water noticeably affected by SSOW is not normally found upriver of about Hammond (RM-8).

In addition to water mass characteristics, suspended sediment and bedform characteristics helped delineate regions (see Chapter 4). During low river discharge, RW has a variable load of mostly inorganic suspended sediment, in concentrations of about 50-100 mg l^{-1}. SSOW is less turbid, with concentrations around 10-40 mg l^{-1}, most of which is biogenous material. Despite these low input values at each end, suspended sediment concentrations in the estuary can reach values as high as 600-1000 mg l^{-1}, in a "turbidity maximum" (TM). Two effects combine to form the turbidity maximum: 1) strong tidal currents act to resuspend silts from the estuary bed, and 2) particulates settling from the upper layers of the water column are transported back into the estuary near the bottom. A circulatory trap for suspended sediment is formed, with the TM most easily seen in near-bottom waters. The TM moves up and down the estuary during the tidal cycle, and the concentrations in the TM vary with tidal current intensities over the neap-spring cycle. The TM is also affected by seasonal discharge fluctuations; its position ranges from about Hammond (RM-8) to upriver of Tongue Point (RM-20) during low riverflow. A chlorophyll discontinuity in surface waters also is found in the Tongue Point area during low riverflow (see Chapter 7), and sinking chlorophyllous particles may add to the near-bottom TM at this time of year.

Most of the estuary bed is composed of medium-to-fine sand and covered with bedforms of some sort: ripples, dunes, sandwaves, etc. (see

Chapter 4). The larger asymmetric bedforms provided an indication of the direction of net sediment transport, averaged over some time period. In the upper estuary, the largest bedforms indicated a predominance of seaward (downriver) transport. During all seasons and at all stages of the tide, the seaward orientation remained unchanged. Consistently seaward-oriented bedforms were also found on the subtidal flanks of most of the channels and on parts of most of the shoals. Bedforms that reverse orientation with each tidal cycle were common in the deep channels near the entrance. However, farther upriver, these channel bedforms maintained an upriver orientation, implying upriver bedload transport. The upriver boundary of these bedforms varied seasonally, but the downriver boundary of upriver bedform orientation was near the seaward tip of Desdemona Sands at all seasons.

Consideration of the above physical and sedimentological characteristics has allowed division of the estuary into eight regions, with the mid-estuarine boundaries of regions 3, 5, 7 and 8 adjustable according to high or low river discharge. The eight major regions are characterized below.

8.1.1 Entrance (Region 1)

The entrance is predominantly deep, with a very high energy level provided by strong tidal currents (greater than 1.5-2 m sec^{-1} on a mean tide) and wave action. The bottom is generally well-sorted, medium-fine sand (mean sizes of 1.75-2.5 phi) that frequently forms linear and wavy-crested bedforms with heights of 30-40 cm and wavelengths of 4-14 m. The bedforms reverse orientation in response to strong tidal currents. Grain size decreases with distance seaward (to approximately 3.00 phi), but silt and clay content remains low. Sediments in the shallow areas of the Entrance Region (ocean beaches and nearshore regions, inner parts of Clatsop Spit) are exposed to ocean waves and are accordingly coarser and better sorted than offshore sediments (2.5 phi). Suspended sediment concentrations are low (less than 50 mg l^{-1}) during low discharge and fair weather conditions, and the suspended material is mainly biogenous. Higher near-bottom concentrations are observed during spring tides, and higher concentrations would be expected in the upper part of the water column during high-discharge conditions.

Water masses involving mixtures of all three water types (SOW, SSOW, and RW) are found here, but the two oceanic water masses predominate except under the highest flow conditions. Stratification is moderate to high under most conditions. The diurnal tide is more important (relative to the semidiurnal tide) than in other parts of the system. Major changes in channel configuration, wave exposure, and circulation patterns have accompanied the installation of the navigation channel/jetty system.

8.1.2 Baker Bay and Trestle Bay (Region 2)

These bays are peripheral to the navigation channel, near the entrance. Energy levels are generally lower in these bays than in the main body of the estuary. This may be attributed to both restricted entrances and the lack of any large net flow.

Sediment size varies significantly between the tidal channels, mudflats, and protected beaches in both bays; the sediments are finer and more poorly sorted than those found in other parts of the estuary. Significant amounts of silt and clay (more than 30%) are found in many samples, and the mean grainsize is fine sand to coarse silt, poorly sorted. Significant deposition has occurred in both bays since the construction of the jetties; both bays displayed an average shoaling of 5 ft (1.53 m) between 1868 and 1935. They remain sites of active fine sediment deposition.

The primary water types influencing these shallow areas are SOW and RW. Stratification is probably minimal except in the deep, middle entrance channel to Baker Bay (Sand Island Gap). The tidal circulation in Baker Bay is complex because of non-linear effects and the three mouths; diverse atmospherically-driven currents and wind-driven sea-surface setups are particularly important in Baker Bay.

8.1.3 Estuarine Channels (Region 3)

This area contains the north and south (navigation) channels, from Clatsop Spit to approximately the upstream limits of significant salinity intrusion (the upstream boundary is seasonally variable).

Sediments in the channels are predominantly medium-fine sand. Sediment size and sorting vary in response to the local current regime; in some places seasonal variations in bottom sediments are observed. Clasts of silty-sand which have been eroded and transported are commonly obtained in estuarine channels. The older source deposits may be of recent origin (possibly thin deposits of fine sediment associated with the settling-out of the turbidity maximum) or older deposits associated with a different channel configuration. The estuarine channel bottoms of the contain a variety of bedforms, ranging from ripples to long sand waves (heights of up to 3 m, wavelength of up to 100 m) which migrate and change character seasonally. Grain size varies with position of many of these bedforms.

Suspended sediment concentrations achieve their highest values in the estuarine channels (up to 600 mg l^{-1} during low discharge conditions) and are highly variable. The turbidity maximum is known to form and advect tidally in this region. Suspended sediment concentrations in the turbidity maximum vary with spring and neap current variations, and the decay of the turbidity maximum during neap tides may contribute to ephemeral fine sediment deposition in the channels.

The primary water types contributing to water mass characteristics are SOW and RW. Tidal exchange is largest in the north channel, where mean tidal current amplitude is 1.5-2.0 m sec^{-1}. The riverflow is greatest in the south channel. Stratification is modest to strong during the high flow season and highly variable during the low flow season. Maximum salinity intrusion occurs during low flow, neap tides.

8.1.4 Youngs Bay (Region 4)

Youngs Bay is tributary to the south channel in the turbidity maximum reach. As with the other peripheral bays (Baker Bay, Grays Bay, Trestle Bay, and Cathlamet Bay), Youngs Bay sediments are relatively fine and poorly sorted.

The primary water types are SOW and RW, but local tributary water is important in the winter season. Stratification is low under most conditions and salt may be totally absent during larger freshets. The energy level is low except in channel areas; net flows are small except during winter storms. Wind and waves are less important than in bays on the north side of the estuary because the fetch is limited for storm winds.

8.1.5 Mid-Estuary Shoals (Region 5)

This predominantly shallow area in mid-estuary consists of shoals separated by shallow channels. Energy levels are moderate to high in most areas. Substantial downstream mean flow occurs in the channels, carrying water from south channel to north channel.

The sediment size in these shoals is generally fine, moderately sorted sand, but grain sizes vary between the numerous small channels (both active and abandoned), shoals, and intertidal portions of this area. Bedforms in a range of sizes (0.3-3.0 m height, 1-100 m wavelength) are found over much of the area. The bedforms tend to be oriented seaward, indicating that most bedload transport is seaward, but upstream transport is found on some shoals and occasionally (during spring flood tides) in some channels. The channels migrate frequently and deposition rates have historically been high in this area.

The primary water types are RW and SOW. Under freshet conditions salt may be absent from most of this reach because salt is confined to the deeper channels. During the low flow season salinity over the flats may be highest on spring tides because of increased mixing, even though salinity intrusion is greater on neap tides in the adjacent channels. Wind and wind waves are in part responsible for the high energy levels.

8.1.6 Grays Bay (Region 6)

Grays Bay is tributary to the north side of the estuary, near or above the upriver limits of salinity distribution (depending on the season).

The sediment sizes are highly variable, ranging from medium sand in some channels to sandy-silt in abandoned channels and mudflats. Bedforms (heights to 1-2 m, wavelengths 40 m) are present in the deep channel off Grays Point and smaller bed features are likely to be found throughout much of the area. Deposition rates have been high in Grays Bay.

SOW, RW, and local tributary flow (winter only) may all be important, but salinity is found only in the deeper channels most of the year and is entirely absent during higher river flows. The tidal exchange for Grays Bay enters through several minor channels, the deepest of which follows the rocky north shore to Portuguese Point. Energy levels range from high in the channels to low in shallow areas. Wind-driven currents, wind waves, and wind setup are all important to the circulatory processes.

8.1.7 Cathlamet Bay (Region 7)

This large and diverse area of sand flats, marsh, and swamp islands separated by channels of varying depth is perhaps less a single entity, at least from a circulatory point of view, than any of the other estuary regions. It has four major connections to the navigation channel downstream of Miller Sands, with sills of various depths. Sediment types vary accordingly. Fine sands and silts are found in marshy intertidal flats, mudflats, and inactive channels. Coarser sediments (medium-fine sand) are found on the more exposed sand flats and inactive channels (e.g., Prairie Channel). Bedforms indicate downstream bedload transport in all of these channels. Significant channel migration has occurred in Cathlamet Bay and fluvial sedimentation processes appear to dominate. Human influences (diking and channel diversion) have resulted in substantial changes to the region.

Salinity intrusion is generally absent, except during low flow periods, when mixed SOW and RW may intrude into the north channel and Tongue Point Basin and (primarily on neap tides) into the other channels south of Miller Sands. Salinity is probably low or absent in shallow areas at all times and only very rarely intrudes into the upper half of the region. Circulation patterns are complex and the energy level quite variable. Tides and riverine processes are both important.

8.1.8 Fluvial Region (Region 8)

The Fluvial Region includes the river channel upriver of significant salinity intrusion, plus associated shallow areas, and continues to the upriver limit of the study area. Sediments from the deep river channels are among the coarsest in the estuary system (0.75-1.50 phi). Grain size tends to increase with depth in the Fluvial Region, with the result that intertidal and shallow sediments are substantially finer but are still sandy (2.5-3.0 phi). Large downriver-oriented bedforms (heights 3 m, wavelengths 100m) occupy the channels and exhibit significant crest/trough grain size variations. In some cases bedforms migrate over a cohesive clay/cobble pavement. The region is dominated by a single river channel, which has been stabilized by permeable dikes. Fluvial sedimentary processes dominate. Suspended sediment concentrations are controlled mostly by upriver sources and vary mainly with discharge and slightly in response to tidal action. Tidal and riverine processes are of nearly equal importance in the reach, except under freshet conditions when the fluvial influence is dominant.

8.2 ESTUARINE HABITAT TYPES

Superimposed through each region are some or all of six habitat types defined principally from biological considerations. These habitat types are shown in Figure 8.1. The water column habitat type (habitat type 1) has been defined as extending from the water surface at mean lower low water (MLLW) to approximately three feet (0.92m) above the estuary bottom. Phytoplankton, zooplankton and free-swimming organisms are found here. Habitat type 2 includes high marsh and swamp areas with irregular tidal inundation, extending from the upper limit of low marsh to the approximate edge of uplands receiving no tidal influence (Thomas, 1983). Important emergent plants are Aster subspicatus, Potentilla pacifica and Agrostis alba. Low marsh (habitat type 3) is characterized as emergent marsh with regular tidal inundation, from the lower limit of high marsh to three feet above MLLW. Important emergent plants include Carex lyngbyei, several species of Scirpus, Deschampsia caespitosa and Juncus balticus. Habitat type 4 includes the tidal flats, from three feet above to three feet below MLLW. Benthic algae predominate here. Habitat type 5 is permanently submerged estuary bottom (including the water column three feet off the bottom) between three and 18 ft (5.52 m) below MLLW. Benthic infauna and epifauna abound here, along with demersal fish. Channel bottom habitat (habitat type 6) is defined as all estuary bottom (plus a contiguous three-foot water column) greater than 18 ft below MLLW. Deeper-dwelling benthic infauna and epifauna can be found here.

The distribution of habitat types in the eight estuarine regions is shown in Table 8.1. The water column habitat type is the only one found in all regions. The channel bottom habitat type is restricted to those regions containing deep channels, and the high and low marsh habitat types are restricted to the bays and the Fluvial Region. The assignment of habitat types to regions as in Table 8.1 is not perfect, as there are some small habitat type remnants in certain regions that have not been considered; for example, there are small amounts of high marsh, low marsh and tidal flat area in the Estuarine Channels Region (region 3). However, the divisions in Table 8.1 fairly depict the major habitat types in each region.

Table 8.1. Distribution of estuarine habitat types within regions.

REGION	1	2	3	4	5	6	7	8
Major	1	1	1	1	1	1	1	1
habitat	4	2	5	2	4	2	2	2
types	5	3	6	3	5	3	3	3
	6	4		4	6	4	4	4
		5		5		5	5	5
							6	6

The areas contained within each habitat type and region are given in hectares in Table 8.2. Region 2 is split into Baker Bay and Trestle Bay for ease in areal computation, but the complete area of any habitat type in region 2 is easily obtained by adding the Baker Bay and Trestle

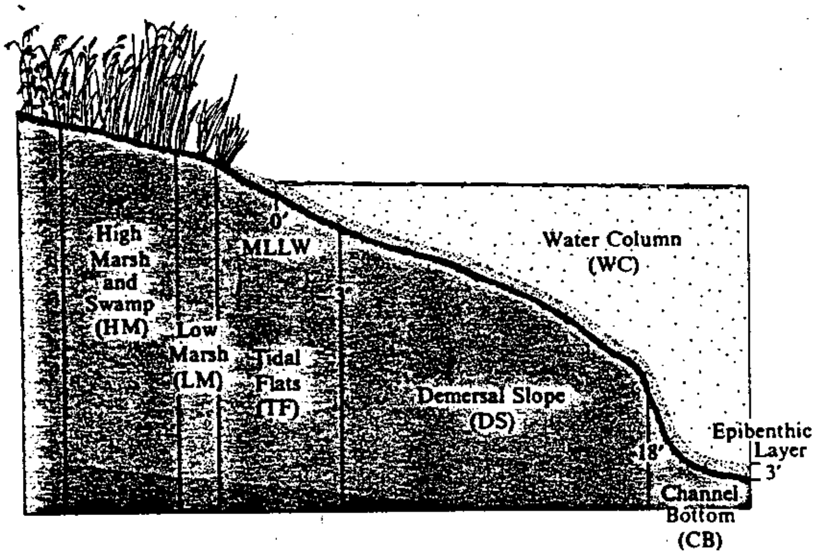


Figure 8.1. Columbia River Estuary habitat types.

TABLE 8.2. Areas of habitat types within each region of the Columbia River Estuary (in hectares). Region 2 includes Baker Bay and Trestle Bay. Regions 3 and 5 include areas that are always in the Estuarine Mixing Zone and areas that are in the Estuarine Mixing Zone only during the low riverflow season. Habitat types are abbreviated as follows: WC = water column, HM = high marsh and swamp, LM = low marsh, TF = tidal flats, DS = demersal slope, CB = channel bottom (planimetered data, CREDDP staff 1983).

REGION/HABITAT TYPE	WC	HM			LM	TF			DS	CB	
	below MLLW	SWAMP	HIGH MARSH	TOTAL	LOW MARSH	above MLLW	MLLW to -3'	TOTAL	-3'to-18'	below-18'	TOTAL
1. Entrance	(3105.01)					97.98	116.97	(214.95)	567.49	2420.55	3202.99
2. Trestle Bay	(163.38)	1.84	58.14	(59.98)	66.51	110.10	144.72	(254.82)	18.66		399.97
Baker Bay	(1490.7)	18.93	20.76	(39.69)	218.79	1225.84	783.86	(2009.70)	692.80	14.04	2975.02
Total	((1654.08))	(20.77)	(78.90)	((99.67))	(285.30)	(1335.94)	(928.58)	((2264.52))	(711.46)	(14.04)	(3374.99)
3. Estuarine Channels											
Estuarine Mixing Zone	(5797.16)	0.58	1.25	(1.83)	1.75	28.46	55.36	(83.82)	1006.42	4735.38	5829.20
Alternating Zones	(1639.73)	4.27		(4.27)	8.34	39.19	26.78	(65.97)	494.34	1118.61	1691.53
Total	((7436.89))	(4.85)	(1.25)	((6.10))	(10.09)	(67.65)	(82.14)	((149.79))	(1500.76)	(5853.99)	(7520.73)
4. Youngs Bay	(1277.32)	49.98	134.66	(184.64)	284.74	473.60	546.98	(1020.58)	679.59	50.75	2220.30
5. Mid-Estuary Shoals											
Estuarine Mixing Zone	(4536.64)				1.75	519.68	567.29	(1086.97)	3318.46	650.89	5058.07
Alternating Zones	(557.41)					23.77	182.15	(205.92)	326.26	49.00	581.18
Total	((5094.05))				(1.75)	(543.45)	(749.44)	(1292.89)	(3644.72)	(699.89)	(5639.25)
6. Grays Bay	(3512.12)	268.42	30.96	(299.38)	274.41	591.87	1386.32	(1978.19)	1820.30	305.50	4677.78
7. Cathlamet Bay	(6036.03)	1756.88	278.84	(2035.72)	1822.80	758.45	1944.23	(2702.68)	3197.29	894.51	10653.00
8. Fluvial Region	(3203.44)	334.01	115.50	(449.51)	174.43	65.61	268.96	(334.57)	958.30	1976.18	3892.99
TOTAL ESTUARY	31,318.94	2434.91	640.11	(3075.02)	2853.52	3934.55	6023.62	(9,958.17)	13079.91	12215.41	41182.03

Bay sub-areas for the specified habitat type. Also, regions 3 and 5 are split depending upon high or low riverflow. Under high flow conditions the Estuarine Mixing Zone alone gives the appropriate areas for any given habitat type; for example, the low marsh area in the Estuarine Channels Region during high flow is 1.75 ha. During low flow conditions the appropriate habitat area is the sum of the Estuarine Mixing and Alternating Zones; thus, the low marsh area in the Estuarine Channels Region under low flow is 1.75 + 8.34 = 10.09 ha. Swamp and high marsh habitat types are combined as habitat type 2 in Table 8.1, so swamp and high marsh areas in Table 8.2 can be summed to yield habitat type 2 area for any given region. In like manner, the area of tidal flat habitat type (habitat type 4) for any region is the sum of the (+3'to 0) and (0 to -3') columns in Table 8.2. Surface area of the water-column habitat type (habitat type 1) is the sum of columns (0 to -3'), (-3 to -18') and (deeper than -18').

8.3 BIOLOGICAL PRODUCTION BY REGIONS AND HABITAT TYPES

Biomass (B) and production (P) of primary producers and consumers are given in Table 8.3 by region and habitat types within each region. (Table 8.3 is located at the end of this chapter). Producers and consumers were divided into functional groups (see Chapter 6), and at times these functional groups were further divided into major sub-groups; thus, predators became one functional category of consumer, and certain infauna, motile macroinvertebrates, larval fish, fish, birds, and mammals were separated as sub-groups of predators. Production:biomass (P/B) ratios were computed when both biomass and production measurements were available (for primary producers). When production was not measured directly (for consumers), P/B ratios were taken from the literature or other data sources and were used to generate production values. The major taxa composing each functional group in each habitat type and region are given in Table 8.4 (located at the end of this chapter).

8.3.1 Producers

Phytoplankton production on a 24-hr basis (i.e., with night-time respiration subtracted) varied from 31.79 gC m^{-2} yr^{-1} in the water column of Youngs Bay to 71.58 gC m^{-2} yr^{-1} in the Fluvial Region. However, mean phytoplankton biomass throughout the year was by far the smallest in Youngs Bay, so that the Youngs Bay P/B ratio was the highest of any of the regions. Conversely, phytoplankton concentration was highest in the Fluvial Region, and the P/B ratio in this region was the lowest of any of the regions. Youngs Bay is thus the most efficient region in producing phytoplankton, because its carbon biomass turns over about 84 times per year, and the Fluvial Region is the least efficient, because its biomass turns over only about 25 times per year. The average P/B ratio for the whole estuary (excluding region 2 for lack of production data) was 38.24 (range of 24.58 to 84.11). Without the very high Youngs Bay ratio, the mean ratio was 30.59 (range of 24.58 to 38.70).

Production of benthic algae in the low marshes and tidal flats (with night-time respiration subtracted) varied between 3.49 and 69.48

gC m^{-2} yr^{-1}, and biomass to 1 cm sediment depth varied between 1.33 and 29.62 gC m^{-2}; however, P/B ratios were remarkably similar (mean P/B was 2.14, with a range of 1.60 to 2.63). Tidal flats of the Entrance Region (Clatsop Spit) had by far the lowest benthic algal production and biomass, but had the highest P/B ratio. Carbon biomass turns over about 2.6 times per year in the Entrance Region. The low marsh habitat type in Youngs Bay had the highest benthic algal production and biomass, and also had a high P/B ratio. The Youngs Bay low marsh thus was very efficient in carrying out its high production. The next highest production and biomass were in the low marsh habitat of Baker and Trestle Bays, and this region had the lowest P/B ratio of any of the regions. Carbon biomass turns over only 1.6 times per year in the low marsh of region 2.

An enormous amount of primary production takes place in the high and low marshes as a result of the seasonal growth of emergent vascular vegetation. Production varied between 237 and 702 gC m^{-2} yr^{-1}, with lowest production in the low marsh of Grays Bay and highest production in the low marsh of Youngs Bay. Production was computed from peak biomass data, so lowest biomass also occurred in the low marshes of Grays Bay and highest biomass in the low marsh habitat of Youngs Bay. Production:biomass ratios were near unity in all regions and habitat types because of computation of production from biomass data.

Mean P/B in phytoplankton was almost 18 times the P/B in benthic algae and about 38 times that in emergent plants. However, comparisons of P/B ratios should not detract from the fact that the emergent vascular plants easily produced the most plant biomass of all the primary producers, on a per unit area basis. Also, habitat types such as the low marshes of Youngs Bay were great producers of plant carbon (by benthic algae as well as emergent plants), even though the efficiency of production was low relative to that in the water column in any region of the estuary.

Using primary production data from Table 8.3 and areal data from Table 8.2, primary production was calculated for each plant-containing habitat type within each region, in metric tons per year (Table 8.5). Total annual primary production for the whole estuary was almost 30,000 MT yr^{-1}, for an average per-unit-area production of 72.8 gC m^{-2} yr^{-1}. If just the water-column primary production is computed, the average annual production drops to almost 68 gC m^{-2} yr^{-1}. This is not productive relative to some other estuaries in the United States and Canada (Table 8.6). Most estimates in Table 8.6 have not been corrected for night-time respiration, and so are not directly comparable to the 68 gC m^{-2} yr^{-1} value for the Columbia River Estuary. If night-time respiratory loss of carbon is added back to the Columbia River value, the rate increases to about 114 gC m^{-2} yr^{-1}, comparable to the estimate for the Fraser River estuary in British Columbia. The Fraser River Estuary is more similar to the Columbia River Estuary than any of the other estuaries in Table 8.6, on the bases of hydrography, topography, circulation, and geographical proximity.

It is interesting to note that the near-coastal ocean waters off Oregon, averaged over the year, are substantially higher (about 300 gC

Table 8.5. Annual net primary production of phytoplankton, benthic algae and emergent vascular plants for each region and habitat in which plants are found in the Columbia River Estuary. Units are metric tons of carbon yr^{-1}.

	PHYTOPLANKTON	VASCULAR PLANTS		BENTHIC ALGAE		
HABITAT:	1	2	3	3	4	TOTAL
REGION						
1	1293.47				3.42	1296.89
2	964.13	261.16	1061.34	119.17	417.77	2823.57
3	3749.60					3749.60
4	481.35	445.72	1998.92	197.84	161.64	3285.47
5	2726.93				70.76	2797.69
6	1609.60	130.63	650.36	73.10	75.05	2538.74
7	3973.66	1037.29	4502.37	265.22	101.56	9880.10
8	2316.53	694.16	542.49	50.15	9.03	3612.36
Total 1		2568.96	8755.48	705.48	839.23	
Total 2	17115.27	11324.44		1544.71		29984.42

Table 8.6. Phytoplankton production in some estuaries and bays of the United States and Canada.

Estuary	$gC\ m^{-2}\ yr^{-1}$	References
Columbia River Estuary, OR.	68(114*)	This study
Fraser River Estuary, B.C.(Can)	120	Parsons _et_ _al_.(1970)
St. Margaret's Bay, N.S. (Can)	190	Platt and Conover (1971)
Bedford Basin, N.S. (Can)	220	Platt (1975)
Narragansett Bay, RI.	310	Furnas _et_ _al_. (1976)
Chesapeake Bay (upper)	125-510	Biggs and Flemer (1972)
Chesapeake Bay (middle)	450-570	Stross and Stottlemeyer (1965)
Chesapeake Bay (lower)	385	Fournier (1966)
Neuse River Estuary, NC.	300-500	Fisher _et_ _al_. (1982)
South River Estuary, NC.	300-500	Fisher _et_ _al_. (1982)
Lower Hudson Estuary, NY.	690-925	O'Reilly _et_ _al_. (1976)

*Annual phytoplankton production in the Columbia River Estuary before night-time respiratory losses were subtracted.

m^{-2} yr^{-1}; Small et al. 1972a, 1972b) than water-column production in the Columbia River Estuary. High coastal production is mainly the result of upwelling during the summer.

8.3.2 Consumers

Wetland Herbivores

Wetland herbivores (Table 8.3) were considered to be dabbling ducks (mainly mallards), muskrat, nutria and beaver (Table 8.4). No data on herbivorous mice or voles, rabbits, or herbivorous insects were available, and deer numbers were not significant enough in the wetlands to warrant attempts at estimating their biomass and production. The avifauna (dabbling ducks) were all considered to be in the low marsh habitat type in the different regions for purposes of calculating biomass and production. Muskrat and nutria were presumed to divide their time equally between high and low marsh, but beaver were presumed to stay in the high marsh/swamp habitat type. These simplistic assumptions can not be rigorously defended, but there is some precedent from the review by Merker and Fenton (1984) and Dunn et al. (1984).

If herbivorous avifaunal production for each region in Table 8.3 is expanded over the total area of low marsh habitat type in each region (Table 8.2), total estuarine production for the herbivorous waterfowl can be estimated at 102,484 gC yr^{-1}, or about 0.10 MT C yr^{-1} (Table 8.7). Annual production by herbivorous mammals can be estimated in the same way, for high marsh and low marsh separately and for total marsh. The high marsh/swamp habitat type supported 4.66 MT C yr^{-1} in furbearer production, while production in the low marsh was estimated at 2.12 MT C yr^{-1}. The total marsh and swamp habitat in the Columbia River Estuary thus supported approximately 6.78 MT C yr^{-1} in furbearer production (Table 8.7). Total production by all wetland herbivores was estimated as 6.88 MT c yr^{-1}.

Deposit Feeders

Deposit-feeding infauna and epibenthic zooplankton were in tidal flat, demersal slope and channel bottom habitats of the various regions. Deposit-feeding infauna represented a substantial amount of carbon production in the estuary, 356.30 MT yr^{-1} (Table 8.7). Of this total, 209.08 MT yr^{-1} was accomplished in the tidal flats, 125.16 MT yr^{-1} in demersal slope areas, and 22.06 in the channel bottom. Corophium was a major contributor to this production. Epibenthic zooplankton, mainly harpacticoid copepods (Table 8.4) were considered to be both deposit feeders and suspension feeders. Somewhat arbitrarily, half the production of these zooplankton was assigned to the deposit feeding category and half to suspension feeding. The production estimate for deposit-feeding zooplankton throughout the estuary was 32.36 MT yr^{-1}, with 12.73 MT yr^{-1} over tidal flats, 11.66 MT yr^{-1} over demersal slope, and 7.97 MT yr^{-1} over the channel bottom. Not all habitat types within all regions were sampled for epibenthic zooplankton, but reasonable estimates could be made for those areas by assuming continuity of production with regions adjacent to those with missing data. This technique was used with several of the animal groups. Production by all

Table 8.7. Total annual carbon production by animal groups in the Columbia River Estuary.

Category	MT C yr^{-1}	MT C yr^{-1}
Wetland avifauna (herbivores)	0.10	6.88
Wetland mammals (herbivores)	6.78	
Deposit-feeding infauna	356.30	388.66
Deposit-feeding epibenthic zooplankton	32.36	
Suspension-feeding zooplankton	2505.52	2,571.89
Suspension-feeding epibenthic zooplankton	32.36	
Suspension-feeding infauna	34.01	
Predatory infauna	61.20	166.98
Predatory motile macroinvertebrates	21.96	
Predatory zooplankton	5.48	
Larval fish (predators)	44.42	
Predatory fish	29.74	
Predatory avifauna	3.96	
Predatory mammals	0.03	
Marine mammals (predators)	0.22	
	TOTAL 3134.44	

deposit feeders totalled 388.66 MT C yr^{-1}.

Suspension Feeders

Suspension-feeding zooplankton, mainly copepods and cladocerans (Table 8.4), made up by far the greatest fraction of animal production in the Columbia River Estuary (Table 8.7). The data base was limited, but the best estimate of estuary-wide production in the water column was 2505.52 MT C yr^{-1}. Numerical estimates of zooplankton in the channel from Jones and Bottom (1984) were combined with estimates from Haertel (1970) and Misitano (1974) in order to arrive at the best possible estuary-wide, seasonally adjusted concentration of animals. Numbers were converted to carbon biomass assuming 0.05 gC animal^{-1}. A P/B ratio of 10 (Parsons et al. 1977) was then applied in order to convert biomass to production. The 2505.52 MT yr^{-1} estimate cannot be very accurate, but is probably the right order of magnitude.

Suspension-feeding epibenthic zooplankton and deposit-feeding epibenthic zooplankton were considered to have the same annual production, 32.36 MT yr^{-1} (Table 8.7). Production was distributed over tidal flats (12.73 MT yr^{-1}), demersal slope (11.66 MT yr^{-1}) and channel bottom (7.97) MT yr^{-1}).

Suspension-feeding infauna were found in tidal flat, demersal slope and channel bottom habitat types. Channel bottom accounted for most of the production (18.32 MT yr^{-1}) because of its extensive area with relatively high concentrations of organisms. Production in tidal flats was 8.71 MT yr^{-1} and in the demersal slope habitat type the production was 6.98 MT yr^{-1}. Total production by suspension-feeding infauna was 34.01 MT yr^{-1} (Table 8.7). Production by all suspension feeders was 2571.89 MT C yr^{-1}.

Predators

Predatory infauna mainly inhabited demersal slope and channel bottom habitat types in the Cathlamet Bay and Fluvial Regions, with large populations also in Cathlamet Bay tidal flats. These large populations, plus smaller ones elsewhere, led to production estimates of 30.47 MT yr^{-1} in channel bottom, 21.68 MT yr^{-1} in demersal slope and 9.05 MT yr^{-1} in tidal flats. Total production by predatory infauna was 61.20 MT yr^{-1} (Table 8.7).

Motile macroinvertebrates were the generally large, non-sedentary species such as crabs (Table 8.4). This group had a total production of 21.96 MT C yr^{-1} in the Columbia River Estuary (Table 8.7). Production was divided into 4.34 MT yr^{-1} on tidal flat areas, 8.95 MT yr^{-1} on demersal slope and 8.67 MT yr^{-1} on the channel bottom.

Omnivorous macrozooplankton such as mysids were considered half as suspension feeders and half as predators. The few numerical data on this group were converted to carbon biomass, and biomass was converted to production using a P/B ratio of 6.0. Another assumption was that the predatory macrozooplankton were restricted to the water column in the saline and brackishwater regions of the estuary (regions 1 through 6).

The production estimate of 5.48 MT C yr^{-1} (Table 8.7) can not be very accurate, but again is probably of the right order.

Larval fish must be an important group of intermediate predators, but again little data were available for production estimates. Numerical concentrations were available in the water column over the navigation channel in region 3 and part way into region 8. Numbers were converted to carbon biomass by assuming 5 mg C per individual larval fish. Biomasses were scaled to the non-channel area in both region 3 and region 8 by two proportions: 1) average channel depth to average depth in the remaining area of the two regions, and 2) the area occupied by the channel to the total area of the region. Expansion to the water columns of the other regions was done by 1) finding the ratio of the area of regions 3 plus 8 to the total estuarine water column area, 2) dividing the carbon biomass of larval fish in regions 3 plus 8 by the ratio of areas determined above, and 3) scaling the estimate by the ratio of water depth in regions 3 plus 8 to average water depth in the estuary. The final estuarine biomass estimate was converted to production by using a P/B ratio of 1.0. The resulting estimate of 44.42 MT C yr^{-1} (Table 8.7) can only be the grossest of estimates, but probably is of the right order.

Sub-adult and adult fish in the estuary, whether in the water column (e.g., salmon) or near the bottom (e.g., flatfish), were all treated as predators (Table 8.4). Reasonable biomass estimates were available for many of the habitat type/region categories in which fish are found in the estuary. Using a P/B ratio of 0.5 allowed estimates of production per m^2 for those categories. For those habitat types or regions in which no data were available, estimates were made. For example, no data were available for the water column in region 5 (Mid-Estuary Shoals). This region is just upriver from region 3 and downriver from region 7, and part of it is adjacent to region 6. Examination of the fish production data for the water columns in these three adjoining regions indicated very similar production values. Presuming continuity of production, the mean of the three per-unit-area production values for the three adjoining regions was used as the best estimate of water-column production per unit area in region 5. Multiplying this per-square-meter value by the area (m^2) of the water-column habitat type in region 5 yielded an estimate of total production in region 5. In like manner, estimates were made for water-column production in regions 2 and 4, and tidal flat production in regions 1 and 7. Complete data sets were available for demersal slope and channel bottom habitat types in all regions containing these habitat types, so no interpolation was required in these cases. Fish production was estimated at 9.73 MT C yr^{-1} in the water column, 6.64 MT C yr^{-1} over the tidal flats, 6.77 MT C yr^{-1} in the demersal slope habitat type, and 6.60 MT C yr^{-1} on channel bottoms, for a grand total of 29.74 MT C yr^{-1} in the estuary (Table 8.7).

Most avifauna in the estuary were considered predatory, even though some bird groups (e.g., gulls) are omnivorous. The mainly herbivorous birds, such as the dabbling ducks, were treated earlier as wetland herbivores. Major predatory bird groups included the diving birds such as western grebes, loons, cormorants, sea ducks, diving ducks and mergansers; the herons; the gulls and terns; sandpipers and shorebirds; crows; and passerine birds most common in or over the marshes, such as swallows, marsh wrens and blackbirds (Table 8.4). Raptors and small passerine birds not commonly associated with the estuary were not considered. Birds were censused on the water, in the marshes and on the tide flats in most of the eight designated estuarine regions. Appropriate live weights were then determined for major bird groups. For example, cormorants were assumed to average 1900 g, western grebes 1476 g, sea ducks (mainly scoters) 950 g, gulls 1136 g, etc. (Hazel et al. 1984). Small birds such as swallows (21 g) and wrens (15 g) obviously contributed much less individual biomass to the estuary than the larger birds.

Avian biomass was converted to carbon biomass by assuming carbon content was 10% of live biomass for all birds. Production was estimated by assuming a P/B ratio of 0.5 for the large birds (herons, ducks, gulls, etc.) and 1.0 for the small birds (swallows, wrens, etc.). Production was estimated at 2.90 MT C yr^{-1} for the open water habitat in the estuary, 0.26 MT yr^{-1} in the marshes, and 0.80 on the tidal flats, for an estuary-wide production of 3.96 MT C yr^{-1} (Table 8.7). The preponderance of carbon production in the water column was mainly the result of the high carbon biomasses of gulls, grebes, cormorants, and other large birds. The small biomasses of swallows, wrens and blackbirds yielded relatively small annual production, even though there were at times great numbers of these birds in the marshes. As always with mobile populations of birds, estimates of abundance and production are imprecise. They certainly vary by season. However, the estimate of average annual production by avifaunal predators appears to be reasonable.

River otter and raccoon were the only predatory land mammals considered, and the raccoon perhaps is more omnivorous than strictly predatory. Other mammals such as shrews were not censused. As expected, the production of river otter and raccoon was slight in the estuary, at 0.03 MT C yr^{-1} (Table 8.7). The animals were never highly concentrated; they were mobile and mainly found in the swamp and high marsh habitat of regions 7 and 8.

It also was difficult to obtain biomass and production estimates for the marine mammals (seals and sea lions), because they are wide-ranging and seasonal in the Columbia River Estuary. For tabular purposes the seals and sea lions were grouped into the water column in the Entrance Region and the Cathlamet Bay Region (Table 8.3). However, only in the Entrance Region were biomasses large enough to use for anything but incidental production estimates. Using a P/B ratio of 0.18 production by marine mammals was 0.007 gC m^{-2} yr^{-1}. Expanding over the water-column area of the Entrance Region yielded a production of 0.22 MT C yr^{-1} (Table 8.7). This production estimate probably was a reasonable annual estimate for the estuary.

Production by all predators in the estuary was estimated at 167.01 MT C yr^{-1}.

8.3.3 Production Comparisons

The annual production estimates in Tables 8.5 and 8.7 can be manipulated in several constructive ways. For example, it is instructive to note that the total estuarine production of all consumer organisms (3134.44 MT C yr^{-1}) was 10.45% of total estuarine primary production (29984.42 MT C yr^{-1}), a not unrealistic figure even though some of the consumers do not consume plant biomass directly. Production by all suspension feeders (2571.89 MT C yr^{-1}) represented 15% of phytoplankton production in the estuary, but only about 2% of the approximately 146,000 MT of the detrital organic carbon carried into the estuary annually.

Production of wetland herbivores apparently was only about 0.06% of total emergent plant production, even though the rate of consumption of marsh vegetation by these wetland herbivores averaged about 10% of emergent plant production (see Chapter 7). Comparison of these two percentages suggests a rate of conversion of consumed material into production (i.e., a gross growth efficiency) that is less than 1%, which is far too low. Either the estimate of herbivore consumption or of emergent plant production is too high, the estimate of herbivore production too low, or some combination of all three. The production by wetland avifauna appears to be low (Table 8.7), as if biomasses of dabbling ducks in the marsh grasses were much underestimated. In addition, grazing pressure by marshland furbearer populations is also very difficult to estimate (Merker and Fenton 1984), and may have been overestimated.

Detailed comparisons above the primary producer and primary consumer trophic levels are impossible to make with the data in hand, because certain predators eat other predators as well as suspension feeders and/or deposit feeders. Also in some cases the major food source for a predator group was not evaluated. For example, swallows consume small flying insects, and this group of prey items was not evaluated. Even so, production by predators must be substantially less than the combined production of deposit feeders and suspension feeders. In the Columbia River Estuary, total predator production (167.01 MT C yr^{-1}) was 5.64% of the combined production of deposit feeders and suspension feeders (2960.55 MT C yr^{-1}).

All infauna, regardless of functional category, had an annual production of 451.51 MT C. Production of all epifauna was 86.68 MT C yr^{-1}, and production in the water column by zooplankton, all fish, and marine mammals was estimated at 2585.38 MT C yr^{-1}. Production in the swamps and marshes by birds and mammals totaled 10.87 MT C yr^{-1}.

The data in Table 8.7 allow other comparisons, if required for specific purposes. It must be kept in mind that these are annual estimates, and cannot easily be fractionated into seasonal or other short-term estimates. Chapter 7 and individual reports must be consulted for this information. Finally, it must be recognized that some of the estimates in Table 8.7 are very much more precise than others, due to the nature of sampling and the nature of the organisms being sampled. Tables 8.3 and 8.7 are useful for first-order comparisons on a yearly basis.

Table 8.3. Biomass and production of functional groups of organisms in habitat types within each of the eight major regions of the estuary. Maximum, minimum and mean biomass are given in units of gC m^{-2}. Production is given as gC m^{-2} yr^{-1}. The production:biomass ratio (P/B) is also calculated when possible. P/B values with an asterisk (*) denote values derived from the literature or other data, and used to estimate production when production was not measured directly. No data is designated "nd". A blank space indicates that the functional group of organisms is not found in that particular region and habitat type, or found very rarely. In some cases a functional group is only found incidentally in a region and habitat type, and is so listed. In cases in which animals are very mobile (e.g. avifauna and marine mammals) their biomass and production estimates have been grouped into "most probable" habitat types within a region or regions.

REGION: 1 (Entrance) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	0.361-2.203 (1.320)	41.011	31.07
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	0.002-0.356 (0.118)	0.059	0.50*
Avifauna	nd	nd	
Marine Mammals	0.010-0.090 (0.040)	0.007	0.18*
Mammals			

REGION: 1 (Entrance) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	1.152-1.503 (1.328)	3.493	2.63
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	Incidental	Incidental	
Mammals			
DEPOSIT FEEDERS			
Infauna	0.012-0.87 (0.063)	0.256	4.05*
Epibenthic Zooplankton	nd	nd	
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	nd	nd	
Infauna	0-0.033 (0.014)	0.057	4.00*
PREDATORS			
Zooplankton			
Infauna	Incidental	Incidental	
Motile Macroinvertebrates	nd	nd	
Larval Fish	nd	nd	
Fish	nd	nd	
Avifauna	nd	nd	
Marine Mammals	[Included in Water Column habitat, Region 1]		
Mammals			

REGION: 1 (Entrance) HABITAT TYPE: 6 (Channel Bottom)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.005-0.312 (0.061)	0.252	4.15*
Epibenthic Zooplankton	0.001-0.019 (0.007)	0.059	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0.001-0.019 (0.007)	0.059	9.00*
Infauna	0-0.217 (0.044)	0.178	4.00*
PREDATORS			
Zooplankton			
Infauna	Incidental	Incidental	
Motile Macroinvertebrates	0-0.212 (0.036)	0.288	8.00*
Larval Fish			
Fish	0.014-0.389 (0.130)	0.065	0.50*
Avifauna			
Marine Mammals			
Mammals			

REGION: 2 (Baker Bay/Trestle Bay) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	nd	41.520	
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 2]		
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	nd	nd	
Avifauna	0.006-0.018 (0.012)	0.006	0.50*
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 2 (Baker Bay/Trestle Bay) HABITAT TYPE: 2 (high Marsh/Swamp)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS	308-330 (319)	331	1.04
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 2]		
Mammals	0.044-0.363 (0.203)	0.142	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	[Included in Low Marsh habitat, Region 2]		
Marine Mammals			
Mammals	Incidental	Incidental	

REGION: 2 (Baker Bay/Trestle Bay) HABITAT TYPE: 3 (Low Marsh)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	14.911-37.687 (26.102)	41.772	1.60
VASCULAR PLANTS	189-692 (370)	372	1.01
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	0-0.010 (0.006)	0.004	0.50*
Mammals	0.036-0.304 (0.170)	0.119	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	0.002-0.004 (0.002)	0.002	1.00*
Marine Mammals	Incidental	Incidental	
Mammals			

REGION: 2(Baker Bay/Trestle Bay) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	4.859-31.851 (18.261)	34.084	1.87
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 2]		
Mammals			
DEPOSIT FEEDERS			
Infauna	0.019-9.852 (3.487)	4.672	1.34*
Epibenthic Zooplankton	0.002-0.019 (0.007)	0.059	9.00*
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	0.002-0.019 (0.007)	0.059	9.00*
Infauna	0.004-0.174 (0.077)	0.309	4.00*
PREDATORS			
Zooplankton			
Infauna	0-0.081 (0.005)	0.005	1.00*
Motile Macroinvertebrates	0-0.120 (0.017)	0.136	8.00*
Larval Fish	nd	nd	
Fish	0.010-0.480 (0.102)	0.051	0.50*
Avifauna	0-0.016 (0.012)	0.012	1.00*
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 2 (Baker Bay/Trestle Bay) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.049-6.661 (2.285)	2.675	1.17*
Epibenthic Zooplankton	0-0.015 (0.006)	0.054	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.015 (0.006)	0.054	9.00*
Infauna	0.010-0.081 (0.043)	0.171	4.00*
PREDATORS			
Zooplankton			
Infauna	0-0.009 (0.003)	0.004	1.35*
Motile Macroinvertebrates	0-0.634 (0.097)	0.775	8.00*
Larval Fish			
Fish	0.001-0.114 (0.048)	0.024	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 3 (Estuarine Channels) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
<u>PRODUCERS</u>:			
PHYTOPLANKTON	0.634-3.320 (2.042)	50.192	24.58
BENTHIC ALGAE			
VASCULAR PLANTS			
<u>CONSUMERS</u>:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	0.040-7.290 (2.176)	21.760	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton	0-0.320 (0.010)	0.060	6.00*
Infauna			
Motile Macroinvertebrates			
Larval Fish	0-7.110 (0.320)	0.320	1.00*
Fish	0.007-0..290 (0.018)	0.024	1.35*
Avifauna	nd	nd	
Marine Mammals	Incidental	Incidental	
Mammals			

REGION: 3 (Estuarine Channels) HABITAT TYPE: 5 (Demeral Slope)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.001-3.064 (0.357)	1.229	3.44*
Epibenthic Zooplankton	nd	nd	
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	nd	nd	
Infauna	0-0.064 (0.022)	0.091	4.20*
PREDATORS			
Zooplankton			
Infauna	0-0.553 (0.025)	0.025	1.00*
Motile Macroinvertebrates	nd	nd	
Larval Fish			
Fish	0.006-0.253 (0.113)	0.057	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 3 (Estuarine Channels) HABITAT TYPE: 6 (Channel Bottom)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.006-0.149 (0.046)	0.177	3.82*
Epibenthic Zooplankton	0-0.049 (0.011)	0.099	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.049 (0.011)	0.099	9.00*
Infauna	0-0.665 (0.047)	0.226	4.80*
PREDATORS			
Zooplankton			
Infauna	0-0.073 (0.006)	0.006	1.00*
Motile Macroinvertebrates	0-0.036 (0.004)	0.029	8.00*
Larval Fish			
Fish	0.008-1.166 (0.151)	0.076	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 4 (Youngs Bay) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	0.091-0.988 (0.378)	31.792	84.11
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 4]		
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	nd	nd	
Avifauna	0.012-0.050 (0.024)	0.012	0.50*
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 4 (Youngs Bay) HABITAT TYPE: 2 (High Marsh/Swamp)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS	nd 319	331	1.04
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 4]		
Mammals	0.044-0.363 (0.203)	0.142	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna			
Marine Mammals			
Mammals	Incidental	Incidental	

REGION: 4 (Youngs Bay) HABITAT TYPE: 3 (Low Marsh)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
<u>PRODUCERS</u>:			
PHYTOPLANKTON			
BENTHIC ALGAE	9.793-36.118 (29.618)	69.479	2.35
VASCULAR PLANTS	392-1011 (702)	702	1.00
<u>CONSUMERS</u>:			
WETLAND HERBIVORES			
Avifauna	0-0.010 (0.004)	0.002	0.50*
Mammals	0.036-0.304 (0.170)	0.119	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	0.004-0.010 (0.008)	0.008	1.00*
Marine Mammals			
Mammals	Incidental	Incidental	

REGION: 4 (Youngs Bay) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	3.607-63.202 (18.445)	34.138	1.85
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 4]		
Mammals			
DEPOSIT FEEDERS			
Infauna	0.332-0.987 (0.652)	2.486	3.81*
Epibenthic Zooplankton	0-0.026 (0.011)	0.095	9.00*
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	0-0.026 (0.011)	0.095	9.00*
Infauna	0-0.044 (0.026)	0.103	4.00*
PREDATORS			
Zooplankton			
Infauna	Incidental	Incidental	
Motile Macroinvertebrates	0-0.045 (0.011)	0.088	8.00*
Larval Fish	nd	nd	
Fish	0.015-0.840 (0.153)	0.077	0.50*
Avifauna	0.004-0.022 (0.012)	0.006	0.50*
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 4 (Youngs Bay) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.006-4.062 (1.463)	2.713	1.85*
Epibenthic Zooplankton	nd	nd	
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	nd	nd	
Infauna	0.006-0.104 (0.034)	0.138	4.00*
PREDATORS			
Zooplankton			
Infauna	Incidental	Incidental	
Motile Macroinvertebrates	nd	nd	
Larval Fish			
Fish	0.022-0.313 (0.098)	0.049	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 5 (Mid-Estuary Shoals) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	0.488-1.961 (1.313)	50.819	38.70
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	nd	nd	
Avifauna	nd	nd	
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 5 (Mid-Estuary Shoals)   HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
<u>PRODUCERS</u>:			
PHYTOPLANKTON			
BENTHIC ALGAE	3.056-11.29 (6.860)	13.017	1.90
VASCULAR PLANTS			
<u>CONSUMERS</u>:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.004-0.319 (0.091)	0.444	4.87*
Epibenthic Zooplankton	0-0.040 (0.013)	0.113	9.00*
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	0-0.040 (0.013)	0.113	9.00*
Infauna	0-0.019 (0.007)	0.031	4.50*
PREDATORS			
Zooplankton			
Infauna	0-0.030 (0.004)	0.004	1.00*
Motile Macroinvertebrates	0-0.004 (0.002)	0.016	8.00*
Larval Fish	nd	nd	
Fish	0.015-3.450 (0.441)	0.221	0.50*
Avifauna	nd	nd	
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 5 (Mid-Estuary Shoals) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.003-0.067 (0.028)	0.112	4.00*
Epibenthic Zooplankton	0-0.074 (0.018)	0.158	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.074 (0.018)	0.158	9.00*
Infauna	0-0.059 (0.017)	0.074	4.35*
PREDATORS			
Zooplankton			
Infauna	0-0.047 (0.008)	0.008	1.00*
Motile Macroinvertebrates	0-0.013 (0.008)	0.060	8.00*
Larval Fish			
Fish	0.002-0.105 (0.036)	0.018	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 3]		
Mammals			

REGION: 6 (Grays Bay) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	0.527-2.502 1.304	39.222	30.08
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 6]		
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	0.024-0.106 (0.057)	0.029	0.50
Avifauna	0.014-0.066 (0.036)	0.026	0.70
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 6 (Grays Bay) HABITAT TYPE: 2 (High Marsh/Swamp)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS	399-442 (420)	422	1.00
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 6]		
Mammals	0.044-0.353 (0.219)	0.153	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	[Included in Low Marsh habitat, Region 6]		
Marine Mammals			
Mammals	nd (0.002)	0.001	0.50*

REGION: 6 (Grays Bay) HABITAT TYPE: 3 (Low Marsh)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	4.408-14.227 (10.428)	26.639	2.55
VASCULAR PLANTS	156-256 (206)	237	1.15
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	0.002-0.010 (0.004)	0.002	0.50*
Mammals	0.036-0.304 (0.170)	0.119	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	0.006-0.010 (0.008)	0.008	1.00*
Marine Mammals			
Mammals	Incidental	Incidental	

REGION: 6 (Grays Bay) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	2.755-14.627 (6.120)	12.680	2.07
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 6]		
Mammals			
DEPOSIT FEEDERS			
Infauna	0.056-0.805 (0.411)	1.972	4.80*
Epibenthic Zooplankton	0-0.194 (0.031)	0.280	9.00*
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	0-0.194 (0.031)	0.280	9.00*
Infauna	0-0.002 (0.001)	0.002	4.00*
PREDATORS			
Zooplankton			
Infauna	0-0.046 (0.026)	0.026	1.00*
Motile Macroinvertebrates	0-0.006 (0.001)	0.008	8.00*
Larval Fish	nd	nd	
Fish	0.015-0.255 (0.084)	0.042	0.50*
Avifauna	0.006-0.008 (0.008)	0.006	0.70*
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 6 (Grays Bay) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.057-1.069 (0.417)	2.018	4.84*
Epibenthic Zooplankton	0-0.071 (0.013)	0.112	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.071 (0.013)	0.112	9.00*
Infauna	0-0.007 (0.003)	0.011	4.00*
PREDATORS			
Zooplankton			
Infauna	0-0.070 (0.022)	0.022	1.00*
Motile Macroinvertebrates	0-0.010 (0.002)	0.012	8.00*
Larval Fish			
Fish	0.003-0.152 (0.062)	0.031	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 7 (Cathlamet Bay) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	0.781-3.245 (1.803)	61.942	34.35
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 7]		
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	0.010-0.118 (0.060)	0.030	0.50*
Avifauna	0.010-0.058 (0.026)	0.014	0.50*
Marine Mammals	Incidental	Incidental	
Mammals			

REGION: 7 (Cathlamet Bay)   HABITAT TYPE: 2 (High Marsh/Swamp)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
<u>PRODUCERS</u>:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS	307-437 (345)	372	1.08
<u>CONSUMERS</u>:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 7]		
Mammals	0.044-0.361 (0.219)	0.153	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	[Included in Low Marsh hiabtat, Region 7]		
Marine Mammals			
Mammals	nd 0.002	0.001	0.50*

REGION: 7 (Cathlamet Bay) HABITAT TYPE: 3 (Low Marsh)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	1.503-13.576 (7.109)	14.548	2.05
VASCULAR PLANTS	146-251 (209)	247	1.18
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	0-0.020 (0.008)	0.004	0.50*
Mammals	0.036-0.304 (0.170)	0.119	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	0.004-0.024 (0.010)	0.010	1.00*
Marine Mammals			
Mammals	Incidental	Incidental	

REGION: 7 (Cathlamet Bay) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	0.802-21.373 (6.245)	13.386	2.14
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 7]		
Mammals			
DEPOSIT FEEDERS			
Infauna	0.034-1.810 (0.222)	1.008	4.54*
Epibenthic Zooplankton	nd	nd	
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	nd	nd	
Infauna	0-0.005 (0.001)	0.002	4.00*
PREDATORS			
Zooplankton			
Infauna	0-4.500 (0.292)	0.292	1.00*
Motile Macroinvertebrates			
Larval Fish	nd	nd	
Fish	nd	nd	
Avifauna	0-0.034 (0.014)	0.010	0.70*
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 7 (Cathlamet Bay) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.005-0.818 (0.327)	0.794	2.43*
Epibenthic Zooplankton	nd	nd	
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	nd	nd	
Infauna	0-0.023 (0.004)	0.016	4.00*
PREDATORS			
Zooplankton			
Infauna	0.006-2.842 (0.573)	0.573	1.00*
Motile Macroinvertebrates	nd	nd	
Larval Fish			
Fish	0.082-0.431 (0.244)	0.122	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 7 (Cathlamet Bay) HABITAT TYPE: 6 (Channel Bottom)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	nd	nd	
Epibenthic Zooplankton	0.003-0.005 (0.004)	0.035	9.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0.003-0.005 (0.004)	0.035	9.00*
Infauna	nd	nd	
PREDATORS			
Zooplankton			
Infauna	nd	nd	
Motile Macroinvertebrates	Incidental	Incidental	
Larval Fish			
Fish	0.010-0.73 0.031	0.016	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 8 (Fluvial Region) HABITAT TYPE: 1 (Water Column)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON	1.704-4.861 (2.891)	71.580	24.76
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 8]		
Mammals			
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton	0.030-1.870 (0.740)	7.410	10.00*
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton	Incidental	Incidental	
Infauna			
Motile Macroinvertebrates			
Larval Fish	0-1.650 (0.200)	0.200	1.00*
Fish	0.009-9.086 (0.037)	0.019	0.50*
Avifauna	0.010-0.054 (0.026)	0.014	0.50*
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 8 (Fluvial Region) HABITAT TYPE: 2 (High Marsh/Swamp)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS	nd (601)	601	1.00
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 8]		
Mammals	0.044-0.363 (0.219)	0.153	0.70*
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	[Included in Low Marsh habitat, Region 8]		
Marine Mammals			
Mammals	nd 0.002	0.001	0.50*

REGION: 8 (Fluvial Region) HABITAT TYPE: 3 (Low Marsh)

Functional Categories	Biomass (B) g C m^{-2}	Production (P) g C m^{-2} yr^{-1}	P/B
	min - max (mean)		
<u>PRODUCERS</u>:			
PHYTOPLANKTON			
BENTHIC ALGAE	2.555-24.496 (12.807)	28.747	2.24
VASCULAR PLANTS	nd (311)	311	1.00
<u>CONSUMERS</u>:			
WETLAND HERBIVORES			
Avifauna	0-0.020 (0.008)	0.004	0.50*
Mammals	0.036-0.304 (0.170)	0.119	
DEPOSIT FEEDERS			
Infauna			
Epibenthic Zooplankton			
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton			
Infauna			
PREDATORS			
Zooplankton			
Infauna			
Motile Macroinvertebrates			
Larval Fish			
Fish			
Avifauna	0.004-0.024 (0.010)	0.010	1.00*
Marine Mammals	Incidental	Incidental	
Mammals			

REGION: 8 (Fluvial Region) HABITAT TYPE: 4 (Tidal Flats)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$ min - max (mean)	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE	2.071-19.904 (5.733)	13.762	2.40
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna	[Included in Low Marsh habitat, Region 8]		
Mammals			
DEPOSIT FEEDERS			
Infauna	0.016-1.083 (0.456)	1.604	3.52*
Epibenthic Zooplankton	0-0.021 (0.006)	0.049	8.00*
SUSPENSION FEEDERS			
Zooplankton	nd	nd	
Epibenthic Zooplankton	0-0.021 (0.006)	0.049	8.00*
Infauna	0-0.020 (0.003)	0.014	4.50*
PREDATORS			
Zooplankton			
Infauna	0.034-0.251 (0.144)	0.144	1.00*
Motile Macroinvertebrates	Incidental	Incidental	
Larval Fish	nd	nd	
Fish	0.030-0.090 (0.054)	0.027	0.50*
Avifauna	0-0.034 (0.014)	0.010	0.70*
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 8 (Fluvial Region) HABITAT TYPE: 5 (Demersal Slope)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.002-0.202 (0.067)	0.318	4.76*
Epibenthic Zooplankton	0-0.012 (0.003)	0.024	8.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.012 (0.003)	0.024	8.00*
Infauna	0-0.009 (0.002)	0.005	2.50*
PREDATORS			
Zooplankton			
Infauna	0-1.263 (0.236)	0.236	1.00*
Motile Macroinvertebrates	Incidental	Incidental	
Larval Fish			
Fish	0.009-0.179 (0.060)	0.030	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

REGION: 8 (Fluvial Region) HABITAT TYPE: 6 (Channel Bottom)

Functional Categories	Biomass (B) $g\ C\ m^{-2}$	Production (P) $g\ C\ m^{-2}\ yr^{-1}$	P/B
	min - max (mean)		
PRODUCERS:			
PHYTOPLANKTON			
BENTHIC ALGAE			
VASCULAR PLANTS			
CONSUMERS:			
WETLAND HERBIVORES			
Avifauna			
Mammals			
DEPOSIT FEEDERS			
Infauna	0.002-0.341 (0.047)	0.195	4.19*
Epibenthic Zooplankton	0-0.010 (0.003)	0.022	8.00*
SUSPENSION FEEDERS			
Zooplankton			
Epibenthic Zooplankton	0-0.010 (0.003)	0.022	8.00*
Infauna	0-0.065 (0.008)	0.017	2.00*
PREDATORS			
Zooplankton			
Infauna	0.009-4.500 (0.800)	0.800	1.00*
Motile Macroinvertebrates	Incidental	Incidental	
Larval Fish			
Fish	0.003-0.171 (0.043)	0.022	0.50*
Avifauna			
Marine Mammals	[Included in Water Column habitat, Region 7]		
Mammals			

Table 8.4. Species occurring in Columbia River Estuary regions and habitat types.

+ = predominant (among the most conspicuous) blank = not present nd = no data

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
PRODUCERS:																																			
PHYTOPLANKTON:																																			
Asterionella formosa	+			+					+			+					+			+					+					+					
Chaetoceros decipiens	+																																		
Coscinodiscus perforatus v. cellulosa	+								+																										
Fragilaria crotonensis	+			+					+			+					+			+					+					+					
Melosira granulata				+					+			+					+			+					+					+					
Melosira italica	+			+					+			+					+			+					+					+					
Skeletonema costatum	+																																		
BENTHIC ALGAE:																																			
Achnanthes hauckiana		nd				nd	+							nd	+							nd					nd	+				nd	+		
Achnanthes lanceolata		nd				nd								nd								nd	+				nd	+				nd	+		
Achnanthes lemmermanni		nd				nd	+							nd	+							nd					nd					nd			
Amphora ovalis		nd				nd								nd								nd					nd	+				nd			
Amphora ovalis v. pediculus		nd				nd								nd								nd	+				nd					nd			
Diatoma tenue v.elongatum		nd				nd								nd	+							nd					nd	+				nd	+		
Fragilaria brevistriata		nd				nd								nd								nd					nd					nd	+		
Fragilaria pinnata		nd				nd								nd	+			+				nd	+				nd	+				nd	+		
Gyrosigma fasciola		nd				nd								nd	+							nd					nd					nd			
Navicula capitata v. hungarica		nd				nd								nd								nd	+				nd	+				nd	+		
Navicula cryptocephala		nd				nd	+							nd	+							nd					nd					nd			
Navicula diserta		nd				nd	+							nd								nd					nd					nd			
Navicula gregaria		nd				nd								nd	+			+				nd	+				nd	+				nd	+		
Navicula minima		nd				nd								nd				+				nd					nd					nd			
Navicula placentula		nd				nd								nd								nd					nd	+				nd			
Navicula pygmaea		nd				nd	+							nd								nd					nd					nd			
Navicula salinicola		nd				nd	+							nd								nd					nd					nd			
Navicula submuralis		nd				nd								nd				+				nd	+				nd	+				nd	+		
Navicula tenuipunctata		nd				nd								nd								nd					nd	+				nd			
Nitzschia frustulum v. perpusilla		nd				nd	+							nd				+				nd					nd	+				nd	+		
Nitzschia hungarica		nd				nd								nd	+							nd					nd					nd			
Nitzschia palea		nd				nd								nd	+			+				nd	+				nd	+				nd	+		
Nitzschia sigma v. sigmatella		nd				nd								nd	+							nd					nd					nd			
Opephora martyi		nd				nd								nd								nd	+				nd					nd			

WC = Water Column
TF = Tidal Shoals and Flats
HM = High Marsh and Swamp
DS = Demersal Slope
LM = Low Marsh
CB = Channel Bottom

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
VASCULAR PLANTS:																																			
Agrostis alba					+	+								+																					
Alisma plantago-aquatica														+													+								
Aster subspicatus					+																	+				+					+	+			
Athyrium felix-femina					+								+																						
Bidens cernua																											+								
Caltha asarifolia																					+														
Carex lyngbyei						+								+							+	+					+					+			
Carex obnupta					+								+																						
Cornus stolonifera																										+					+				
Deschampsia caespitosa						+															+	+				+	+				+	+			
Eleocharis palustris														+								+					+					+			
Elodea canadensis																						+	+												
Equisetum fluviatile																											+								
Festuca arundinacea																					+					+					+				
Impatiens capensis																										+					+				
Juncus balticus						+																+										+			
Juncus oxymeris																						+					+					+			
Lathyrus palustris					+								+																						
Lilaeopsis occidentalis						+																+										+			
Lonicera involucrata													+																						
Lotus corniculata																					+					+					+				
Lysichitum americanum																										+					+				
Mentha piperita																					+														
Oenanthe sarmentosa					+	+							+	+																					
Picea sitchensis													+																						
Potamogeton richardsonii																								+											
Potentilla pacifica					+								+								+														
Rubus spectabilis													+																						
Sagittaria latifolia																						+					+					+			
Salix hookeriana													+																						
Salix lasiandra																										+					+				
Salix sitchensis																										+					+				
Scirpus acutus						+																					+								
Scirpus americanus						+																													
Scirpus microcarpus																					+														
Scirpus validus						+								+								+					+					+			
Sium suave																					+						+					+			
Spiraea douglasii																										+					+				
Triglochin maritinum						+																													
Typha angustifolia						+								+													+					+			
Typha latifolia																																+			
Zostera marina							+																												
Zostera japonica							+																												

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
CONSUMERS:																																			
ZOOPLANKTON																																			
(Suspension Feeders):																																			
Acartia clausii	nd			nd					+			nd					nd			nd					nd										
Acartia longiremis	nd			nd					+			nd					nd			nd					nd										
Barnacle nauplii	nd			nd					+			nd					nd			nd					nd										
Bivalve larvae	nd			nd					+			nd					nd			nd					nd										
Bosmina longirostris	nd			nd					+			nd					nd			nd					nd					+					
Calanus pacificus	nd			nd					+			nd					nd			nd					nd										
Centropages abdominalis	nd			nd					+			nd					nd			nd					nd										
Ceriodaphnia pulchella	nd			nd								nd					nd			nd					nd					+					
Cyclops bicuspidatus v. *thomasi*	nd			nd					+			nd					nd			nd					nd					+					
Cyclops vernalis	nd			nd					+			nd					nd			nd					nd					+					
Daphnia gateata v. *mendotae*	nd			nd					+			nd					nd			nd					nd					+					
Daphnia pulex	nd			nd					+			nd					nd			nd					nd					+					
Diaptomus ashlandi	nd			nd					+			nd					nd			nd					nd					+					
Diaptomus brachyurum	nd			nd					+			nd					nd			nd					nd					+					
Diaptomus franciscanus	nd			nd					+			nd					nd			nd					nd					+					
Diaptomus novamexicanus	nd			nd					+			nd					nd			nd					nd					+					
Eogammarus confervicolus	nd			nd					+			nd					nd			nd					nd										
Euphausiacea nauplii	nd			nd					+			nd					nd			nd					nd										
Eurytemora affinis	nd			nd					+			nd					nd			nd					nd					+					
Evadne nordmanni	nd			nd					+			nd					nd			nd					nd										
Gastropod larvae	nd			nd					+			nd					nd			nd					nd										
Oikopleura dioica	nd			nd					+			nd					nd			nd					nd										
Oithona similis	nd			nd					+			nd					nd			nd					nd										
Paracalanus parvus	nd			nd					+			nd					nd			nd					nd										
Podon leucharti	nd			nd					+			nd					nd			nd					nd										
Pseudocalanus elongatus	nd			nd					+			nd					nd			nd					nd										
(Predators):																																			
Archaeomysis grebnitzkii	nd			nd					+			nd					nd			nd					nd										
Neomysis mercedis	nd			nd					+			nd					nd			nd					nd					+					
Sagitta elegans	nd			nd					+			nd					nd			nd					nd										

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
LARVAL FISHES:																																			
Cottus asper	nd			nd					+			nd					nd			nd					nd					+					
Engraulis mordax	nd			nd					+			nd					nd			nd					nd										
Osmeridae	nd			nd					+			nd					nd			nd					nd					+					
EPIBENTHIC INVERTEBRATES																																			
(Deposit Feeders):																																			
Alonella sp.																							+										+		
Attheyella sp.																							+										+	+	+
Bryocamptus spp.							+	+																											
Candona sp.																																	+		
Chironomidae																							+											+	
Corophium spp.			+															+					+	+									+	+	
Ectinosomatidae			+				+	+			+				+			+	+				+	+									+	+	
Eogammarus confervicolus								+																											
Huntemannia jadensis																		+																	
Laophontidae							+								+								+												
Leucon sp.								+																											
Limnocythere sp.											+							+					+	+									+	+	
Microarthridion littorale			+				+				+				+			+					+												
Nematomorphii																																			+
Paraleptastacus sp.																			+																
Podocopa																								+									+		
Scottolana canadensis			+				+	+			+				+			+	+				+	+										+	
Tachidius discipes																							+												
Tachidius triangularis							+	+							+			+	+															+	
(Predators):																																			
Cancer magister			+				+	+			+																								
Crangon franciscorum			+				+	+			+				+			+	+				+	+					+						
Neomysis mercedis			+				+				+							+	+				+	+									+	+	+
(Suspension Feeders):																																			
Acartia clausii			+																+																
Alona spp.																																	+	+	
Balanomorpha (*Cypris*)			+				+	+			+				+																				
Bosmina sp.			+								+							+	+					+					+				+	+	+
Cyclops bicuspidatus			+					+			+				+			+	+				+	+					+				+	+	+
Cyclops vernalis			+								+				+			+	+				+	+					+				+	+	+
Daphnia spp.											+																		+				+	+	+
Diaptomus sp.			+								+				+								+	+									+	+	+
Eurytemora affinis			+				+	+			+				+			+	+					+										+	+
Halicyclops sp.																																	+		
Oithona sp.			+																+																
Paracyclops fimbriatus																							+												
Rotifera			+					+			+								+				+	+					+				+		+

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
BENTHIC INFAUNA																																			
(Deposit Feeders):																																			
Chironomidae																							+	+				+	+				+	+	+
Corophium salmonis										+					+	+		+	+				+	+				+	+				+	+	+
Eohaustorius estuarius										+								+	+																
Fluminicola virens																							+	+				+	+				+	+	
Goniobasis plicifera																							+					+					+		
Hobsonia florida							+	+							+																				
Macoma balthica							+	+			+				+																				
Neanthes limnicola		+					+	+			+				+	+		+											+					+	
Oligochaeta							+	+							+	+		+					+	+				+	+				+	+	+
Paraonella platybranchia			+																																
Paraphoxus milleri		+	+							+	+																								
Pseudopolydora kempi							+																												
Spio spp.			+																																
(Suspension Feeders):																																			
Corbicula manilensis																							+	+				+	+				+	+	+
Mya arenaria							+																												
(Predators):																																			
Eogammarus confervicolus										+	+					+		+	+																
Eteone spp.		+					+	+																											
Heleidae																								+				+	+				+	+	+
Nephtys californiensis			+																																
Rhynchocoela		+	+					+		+	+				+	+		+	+				+	+											+
Saduria entomon																		+																	
Turbellaria		+					+	+							+																				

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
FISH (Predators):																																			
<u>Acipenser</u> <u>transmontanus</u>		nd																										nd	+	+					
<u>Allosmerus</u> <u>elongatus</u>	+	nd																		+								nd							
<u>Alosa</u> <u>sapidissima</u>	+	nd		+					+			+								+					+			nd		+					
<u>Ammodytes</u> <u>hexapterus</u>		nd	+																									nd	+						
<u>Catostomus</u> <u>macrocheilus</u>		nd																						+				nd	+						
<u>Citharichthys</u> <u>stigmaeus</u>		nd						+							+													nd							
<u>Clupea</u> <u>harengus</u> <u>pallasi</u>	+	nd							+			+								+					+			nd							
<u>Cottus</u> <u>asper</u>		nd						+		+	+				+	+		+	+				+	+				nd	+					+	+
<u>Cymatogaster</u> <u>aggregata</u>		nd						+		+	+				+	+		+	+				+	+				nd	+				+	+	
<u>Engraulis</u> <u>mordax</u>	+	nd																										nd							
<u>Gasterosteus</u> <u>aculeatus</u>	+	nd		+					+			+					+			+					+			nd		+					
<u>Hypomesus</u> <u>pretiosus</u>	+	nd							+			+								+					+			nd							
<u>Isopsetta</u> <u>isolepsis</u>		nd	+																									nd	+						
<u>Lampetia</u> <u>azresii</u>		nd																		+								nd							
<u>Leptocattus</u> <u>arinatus</u>		nd						+		+	+				+	+		+	+				+	+				nd	+				+	+	+
<u>Lumpenus</u> <u>sagitta</u>		nd	+					+			+																	nd							
<u>Microgadus</u> <u>proximus</u>		nd	+					+			+																	nd							
<u>Mylocheilus</u> <u>caurinus</u>		nd	+							+	+				+	+			+				+	+				nd	+						+
<u>Oncorhynchus</u> <u>kisutch</u>	+	nd		+					+			+					+			+					+			nd		+					
<u>Oncorhynchus</u> <u>nerka</u>	+	nd							+																			nd							
<u>Oncorhynchus</u> <u>tshawytscka</u>	+	nd		+					+			+					+			+					+			nd		+					
<u>Parophrys</u> <u>vetulus</u>		nd	+					+			+				+	+		+	+				+	+				nd	+				+	+	
<u>Platichthys</u> <u>stellatus</u>		nd	+							+	+				+	+		+	+				+	+				nd	+				+	+	+
<u>Psettichthys</u> <u>melanostictus</u>	+	nd																										nd							
<u>Salmo</u> <u>clarki</u>	+	nd	+					+	+		+																	nd							
<u>Salmo</u> <u>gairdneri</u>	+	nd		+					+			+					+			+					+			nd		+					
<u>Spirinchus</u> <u>thaleichthys</u>	+	nd	+					+	+		+	+								+					+			nd		+					
<u>Thaleichthys</u> <u>pacificus</u>	+	nd		+					+			+								+					+			nd		+					

TAXON Region:	Entrance			Baker Bay & Trestle Bay					Estuarine Channels			Youngs Bay					Mid-Estuary Shoals			Grays Bay					Cathlamet Bay					Fluvial Region					
Habitat Types:	WC	TF	CB	WC	HM	LM	TF	DS	WC	DS	CB	WC	HM	LM	TF	DS	WC	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	WC	HM	LM	TF	DS	CB
AVIFAUNA (Predators):																																			
Aechmophorus occidentalis				+								+								+					+					+					
Azelaius phoeniceus																					+	+				+	+				+	+			
Ardea herodias					+	+	+					+	+	+	+						+	+	+			+	+	+			+	+	+		
Aythya valisineria				+			+													+					+					+					
Calidris alba							+																												
Calidris alpina							+														+	+	+			+	+	+			+	+	+		
Calidris mauri					+	+	+								+						+	+	+			+	+	+			+	+	+		
Calidris minutilla					+	+	+								+						+	+	+												
Cistothorus palustris							+						+	+												+	+				+	+			
Corvus brachyrhynchus							+						+	+	+						+	+	+			+	+	+			+	+	+		
Geothlypis trichas													+	+																					
Hirunda rustica				+			+						+	+	+					+	+	+	+		+	+	+	+		+	+	+	+		
Iridoprocne bicolor													+	+						+	+	+			+	+	+	+		+	+	+	+		
Larus californicus				+								+			+						+	+	+			+	+	+			+	+	+		
Larus canus				+								+			+					+	+	+	+		+	+	+	+		+	+	+	+		
Larus delawarensis				+	+	+	+					+			+					+	+	+	+		+	+	+			+	+	+			
Larus glaucescens				+											+						+	+	+			+	+				+	+			
Larus occidentalis				+			+								+					+	+	+	+			+	+				+	+			
Larus philadephia				+			+													+															
Melanitta perspicillata				+																															
Petrochelidon pyrrhonota																				+	+	+	+			+	+				+	+			
Phalacrocorax auritus				+								+								+					+					+					
Porzana carolina													+	+																					
Sterna cuspia				+																					+					+					
Tachycineta thalassina													+	+						+	+	+	+			+	+				+	+			
(Wetland Herbivores):																																			
Anser acuta																										+	+				+	+			
Anser americana																										+	+				+	+			
Anser platyrhynchos				+	+	+	+					+	+	+	+					+	+	+	+		+	+	+	+		+	+	+	+		
MARINE MAMMALS (Predators):																																			
Eumetopias jubatus	+	+	+	+			+	+	+	+	+	+			+	+	+	+	+	+		+	+		+			+	+	+			+	+	+
Phoca vitulina	+	+	+	+			+	+	+	+	+	+			+	+	+	+	+	+		+	+		+			+	+	+			+	+	+
Zalophus californianus	+	+	+	+			+	+	+	+	+	+			+	+	+	+	+	+		+	+		+			+	+	+			+	+	+
TERRESTRIAL/AQUATIC MAMMALS																																			
(Wetland Herbivores):																																			
Castor canadensis					+	+							+	+							+	+				+	+				+	+			
Myocastor coypus					+	+	+						+	+	+						+	+	+			+	+	+			+	+	+		
Ondatra zibethicus					+	+	+						+	+	+						+	+	+			+	+	+			+	+	+		
(Predators):																																			
Lutra canadensis					+	+	+						+	+	+						+	+	+			+	+	+			+	+	+		
Procyon lotor					+	+	+						+	+	+						+	+	+			+	+	+			+	+	+		

9. SUMMARY AND CONCLUSIONS

The intent throughout preceding chapters of this synthesis has been to develop an integrated view of interactions between the complex circulation and sedimentation processes of the estuary and the structure and dynamics of its biotic community. The purpose of the following discussion is to synthesize these diverse relationships into a more holistic understanding of the Columbia River estuarine ecosystem. An ecosystem perspective will make it possible to evaluate the relative importance of the various estuarine habitats and biota, historical and future human impacts and the future research required to resolve gaps in our understanding of the dynamics of this estuary.

These conclusions should be viewed from two perspectives--their scientific importance and the implications for future estuarine water and land uses. For a variety of reasons, physical and biological processes in the Columbia River Estuary cannot be explained by the traditional scientific concepts which originated in the less-energetic estuaries of the east coast of North America and northern Europe. The results of our process-oriented interpretation of the estuarine ecosystem emphasize the need for better understanding of the dynamics of the diverse estuaries along the rim of the northeastern Pacific Ocean. The Columbia River estuarine ecosystem is very different from the better-known Atlantic estuaries such as Narragansett Bay and Chesapeake Bay, because different and highly energetic physical processes operate and dominate the structure and direction of biological processes. Although estuaries in the Pacific Northwest also differ from one another and must be considered individually in the context of their own geologic, hydrologic, and oceanographic settings, many of the basic physical and ecological processes identified in this study of the Columbia River Estuary may be applicable to other estuaries of the Pacific Northwest.

9.1 SUMMARY

9.1.1 Circulation

The high river discharge, substantial supplies of suspended and bedload sediment, neap-spring variations in tidal energy, variable density structure and mixing processes, near-bottom turbidity maximum, and morphology of the Columbia River estuary interact to produce a predominantly low-salinity, sandy estuarine system in which only a small fraction of the fine-grained material entering the system is retained.

The primary tidal circulation occurs at diurnal and semidiurnal frequencies and is driven by the oceanic tides and the time-varying density distribution. Bottom friction and the resulting downward flux of momentum to the bed affect the entire flow under many conditions. The secondary circulation represents a modifying feature of primary circulation. It can be divided into three components that occur at different frequencies: (1) the tidal overtones which occur at frequencies higher than semidiurnal and are produced by the distortion of the tidal wave as it moves upriver; (2) the secondary tidal circulation which occurs at diurnal and semi-diurnal frequencies; and (3) the nearly steady residual circulation or mean flow. The mean flow is driven by riverflow, the density distribution, and tidal energy transferred from the primary circulation. Atmospheric effects do not play a major role in the residual circulation in this estuary.

The primary tidal circulation provides most of the energy for circulatory processes and sediment transport in the estuary, but most of this tidal energy is dissipated below RM-20. In the fluvial part of the system, most of the energy is derived from the potential energy of the mean flow (energy released as water flows downhill). Both sources of energy are important in the middle, tidal-fluvial reaches; however, it is in these reaches of the upper estuary that the lowest total energy levels are found. Energy is most rapidly dissipated near the entrance and in shallow reaches of the estuary and river.

The salinity distribution within the estuary is maintained in the face of strong river discharge primarily by tidal currents working on the horizontal salinity gradient; inward transport by the mean flow is of secondary importance. Furthermore, mixing and tidal processes, rather than entrainment, are principally responsible for the vertical transport of salt. Maximum salinity intrusion occurs under low-flow, neap tide conditions because of the greater stratification at that time.

Due to the configuration of the two major channels, water and salt transport is quite asymmetric. Salt is transported into the estuary primarily by the strong tidal exchange in the north channel and out of the estuary primarily by the mean flow in the south channel. Thus, high-salinity, estuarine water is cycled (and perhaps recycled) inward in the north channel, across the mid-estuary shoals, and outward in the south channel.

Circulation in shallow areas and the peripheral bays is less energetic than that in the major channels because both tidal and mean flows are lower. Salinity intrusion into such non-channel habitats is sporadic and highly variable, especially at the upstream limits of salinity intrusion (e.g. Cathlamet and Grays Bays), and is influenced primarily by tidal range and riverflow.

9.1.2 Sedimentation

Most of the medium and fine sand supplied by the river is retained within the estuary. Thus, long-term accumulation in the estuary consists of tidal and fluvial deposits of predominantly bedload materials. Only about 20% of the finer sediments supplied to the estuary (very fine sand, silt, and clay) is permanently deposited there; most deposition of fine-grained sediments occurs in the peripheral bays and inactive channels. High concentrations of suspended sediment occur in the turbidity maximum located just seaward of the upstream limit of salinity intrusion. The turbidity maximum is advected with the tidal currents; the mean position of the turbidity maximum changes with the fortnightly tidal variations and discharge fluctuations. Neap-spring variations in suspended sediment concentrations are substantial;

material that is temporarily deposited during periods of weak tides is resuspended during spring tides. Lateral transport to peripheral bays and subsequent settling of suspended sediments from the turbidity maximum may be an important mechanism of accumulation of fine sediment. On the mid-estuary shoals, adjacent to the mean position of the turbidity maximum, energy levels are too high to permit long-term deposition of silts and clays, but these habitats are exposed to high rates of fine-sediment flux. Overall, while the relatively little fine sediment is ultimately retained in the estuary, the turbidity maximum processes tend to produce residence times of suspended sediment that are longer than that of non-settling particles, and are probably on the order of a few days to two weeks (half a tidal month). Both the mean position of the turbidity maximum and a node in bedform transport occur near the upstream limits of upstream bottom flow.

Although most of the energy for circulation and sediment transport in the estuary is provided by tidal currents, sedimentation and erosion are determined by convergence and divergence of the bottom shear stress and the mean flow. Determination of the mean flow distribution, therefore, was a major objective of the physical studies. The magnitude of the mean flow through the estuary is determined by the riverflow plus Stokes drift compensation flow. The vertical distribution of this Eulerian mean flow is determined by differences in structure of the flood and ebb currents. These are, in turn, governed by stratification, horizontal salinity gradient, bottom friction, and topographic effects. Because of the topographic complexity and the temporal and spatial variability of the horizontal salinity gradient, numerical models were necessary to determine the distribution of the mean flow and salinity. Neap-spring and seasonal variations in mean flow are substantial. Upstream bottom flow is most prominent during low-flow neap tides when stratification and salinity intrusion are large. Upstream bottom flow is not always continuous from the entrance to the mean position of the 1 ppt salinity contour, but may be interrupted by regions of downriver mean flow.

Divergences and convergences in the mean flow determine the location of the turbidity maximum and the patterns of bedform transport. Model results indicate that the salinity structure and mean flow divergences/convergences are closely associated with bottom topography. The discontinuity of the mean upriver bottom flow, especially in the south channel, results in several flow convergences generally associated with positive bathymetric features (e.g. shoals). Channel bottom bathymetry creates convergences in bottom flow which are reinforced by further shoaling; in comparison, flow divergences maintain bottom depressions. Thus, the mean flow and the bottom bathymetry tend to maintain and reinforce each other within the region of the estuarine circulation. The existence of multiple flow divergences/convergences in part explains the presence of tidally-reversing bedforms in the entrance region, even though flood-oriented bedforms (upstream transport) are found further upriver, between the entrance and the fluvial reach. Bedforms in the fluvial reach are always oriented downriver.

Three broad sedimentary regimes exist as determined by tidal energy, river discharge, or net upstream bottom flow dominance of the transportation and deposition of sediments; these are the entrance, the estuarine mixing, and the tidal-fluvial zones. Tidal flat and demersal slope sedimentation near the entrance is influenced by local and ocean waves and by sediment supply. The energy budget for the estuary and river system indicates that an energy minimum is located in the upper estuary. In this region, the total energy available from the tidal circulation and riverflow is lower than elsewhere in the system. It is in this region that the long-term sedimentation of bedload material occurs.

9.1.3 Primary Production

Physical conditions, rather than biological interactions such as herbivory or competition, appear to regulate the occurrence, distribution, and production of autotrophs in the estuary.

Primary producers are mainly restricted to wetland (swamp and marsh) vascular plants, phytoplankton in the water column, and benthic microalgae on littoral and shallow sublittoral habitats. Unlike coastal marine habitats and other estuaries in the Pacific Northwest, submergent vascular plants (eelgrass) and macroalgae are relatively rare, and their contribution to total primary production in the estuary is comparatively unimportant. The low surface salinity, high turbidity, low light levels, and active sediment transport in the estuary are factors which may severely limit the occurrence of submergent vascular plants and macroalgae.

Emergent vascular plants characterizing the extensive marsh habitats in the estuary were separated into six assemblages representing low and high elevation marshes in brackish water and freshwater regions of the estuary. Brackish water, low marsh assemblages dominated by *Carex lyngbyei*, *Lathyrus palustris*, *Potentilla pacifica*, *Juncus balticus*, *Agrostris alba*, *Triglochin maritinum*, *Scirpus americanus*, and *Eleocharis palustris* were found at the greatest number of sampling sites throughout the estuary. These assemblages were closely associated with low marsh sites in the middle of the estuary and with the *Typha latifolia* marsh in the tidal-fluvial zone. In contrast, high marsh sites in the estuarine mixing zone which were dominated by *Oenanthe sarmentosa*, *Lotus corniculatus*, *Mimulus guttatus*, *C. lyngbyei*, and *Deschampsia caespitosa* constituted separate assemblages, as did a unique low marsh assemblage characterized by *Myosotis laxa* and *Isoetes echinospora*. It should be noted, however, that there was considerable overlap among most of these assemblages and some emergent plants (i.e. *Carex lyngbyei*) were generally ubiquitous throughout the estuary's marsh habitats.

On an areal basis, net annual primary production by the emergent vascular plant assemblages was much higher than either phytoplankton or benthic microalgae, averaging between about 237 gC m^{-2} yr^{-1} in the low marshes of Grays Bay and 702 gC m^{-2} yr^{-1} in the low marshes of Youngs Bay.

Net annual phytoplankton production within the estuary, with nighttime respiratory losses subtracted from net daytime production, ranged from about 32 gC m^{-2} yr^{-1} in the Youngs Bay water column to about 72 gC m^{-2} yr^{-1} in the tidal-fluvial zone. The mean for the estuary, weighted by area, was 68 gC m^{-2} yr^{-1}. Without nighttime respiratory losses of carbon, net annual daytime production, weighted by area, averaged about 114 gC m^{-2} yr^{-1}. These annual estimates of areal production were low relative to most other estuaries in the United States and Canada, but the daytime production value was comparable to the Fraser River estuary in British Columbia, Canada, which is also comparable to the Columbia River Estuary in terms of its physical attributes and processes.

Freshwater phytoplankton taxa apparently were lysed and converted to dead, non-chlorophyllous detrital particles at 0 to 5 ppt isohalines at the upstream boundary of the turbidity maximum. This "phytoplankton sink" undoubtedly included much of the estimated phytoplankton carbon "losses" within the estuary. Disregarding the effects of the May 1980 Mount St. Helens eruption, approximately 5.6×10^{4} MT yr^{-1} of phytoplankton carbon, on average, entered the estuary from the Columbia River, compared to 1.7×10^{4} MT C yr^{-1} which was produced in the estuarine water column. Grazing losses in the estuary via suspension-feeding zooplankton were estimated to be only 0.1×10^{4} MT C yr^{-1}. Approximately 2.2×10^{4} MT yr^{-1} of phytoplankton carbon was "lost" in the estuary, probably due mainly to sinking and/or formation of detritus at the freshwater-brackish water interface adjacent to the turbidity maximum. This loss represented an 86% loss from the potential phytoplankton carbon flux through the estuary but represents a significant flux of dissolved and fine particulate carbon to the "microbial loop" controlling detritus-based food webs (Azam et al. 1983).

Light is the principal factor regulating the rate of phytoplankton primary production in the estuary, both because of the seasonal variations in the intensity of solar radiation and the extent of attenuation within the water column. Of the critical inorganic nutrients measured, only nitrate was depleted (during the summer) to the point of potential limitation of phytoplankton production. However, other nitrogen forms such as ammonia were not measured, so nitrogen may not be limiting to phytoplankton production.

Benthic microalgae are most prominent as diatom flora on the littoral flats and as a comparatively less developed blue-green algal flora among the emergent vascular plants in the low marsh habitat. Analysis of the taxonomic composition indicated that benthic microalgae in littoral flat habitats in Cathlamet Bay and Fluvial Regions are predominantly freshwater forms. Assemblages at Youngs Bay, in the central region of the estuary, are transitional between freshwater (including planktonic) and estuarine forms. Microflora in the lower portion of the estuary in the region of Baker Bay are exclusively estuarine.

The highest mean biomass (about 25 ug chlorophyll *a* cm^{-3}) of benthic microflora occurred in the Youngs Bay-Baker Bay region, declining to about 10 ug cm^{-3} in the Fluvial Region and about 1 ug cm^{-3} in the Entrance Region. Benthic gross primary production generally reflected a similar pattern, from about 84 mgC m^{-2} hr^{-1} in Youngs Bay to about 30 mgC m^{-2} hr^{-1} in the Fluvial Region and about 5 mgC m^{-2} hr^{-1} in the Entrance Region. Net annual production, with nighttime respiration acccounted for, ranged from 3.4 gC m^{-2} yr^{-1} at Clatsop Spit to 69.5 gC m^{-2} yr^{-1} on the tidal flats of Youngs Bay. Although microfloral biomass remained relatively stable throughout the year, mean rates of benthic primary production showed seasonal maxima between March and October. Moreover, rates were higher in the low marshes and higher elevations of the littoral flats than in the lower elevations.

Extrapolated over the 41,182 ha total estuarine area, the total estimated net primary production for the region was 3.0 X 10^4 MT C yr^{-1}, or approximately 0.7 MT ha^{-1}. Because the water column encompassed such a large area compared to marshes, swamps, and tidal flats, phytoplankton (1.7 X 10^4 MT; 57%) dominated annual production. Emergent vascular plants (1.1 X 10^4 MT; 38%) followed, and production of benthic microalgae (0.2 X 10^4 MT; 5%) was relatively small because of the restricted area of tidal flat habitat in the estuary and their comparatively low productivity. Total net primary production from all plant sources within the estuary was just slightly less than the estimated import of phytoplankton-derived particulate carbon into the system (5.6 X 10^4 MT C yr^{-1}).

9.1.4 Detritus

Although there was no CREDDP research directed toward the origins, fates, or fluxes of detritus within the estuary, estimates of suspended detrital carbon concomitant to phytoplankton studies indicated that about 14.6 X 10^4 MT C yr^{-1} was imported into the estuary and approximately 15.9 X 10^4 C yr^{-1} were exported from the system. In addition to the direct detrital carbon input, approximately 3.9 x 10^4 MT C yr^{-1} was estimated to be added to the estuary from the death of living phytoplankton that were either imported as live phytoplankton or produced within the estuary. In addition, the total emergent vascular plant production of about 1.1 X 10^4 MT C yr^{-1}, minus that consumed by wetland herbivores (0.04 to 0.3 x 10^4 MT C yr^{-1}) was presumed to die back each autumn and eventually enter the detritus pool. Thus, if detrital input from the small amount of benthic algal production is assumed to be insignificant, slightly over 3 X 10^4 MT C yr^{-1} was presumed to accumulate and/or be utilized by estuarine heterotrophs and primary consumers. Obviously, this is more than sufficient to account for the estimated 0.2 x 10^4 C yr^{-1} consumed by estuarine deposit feeders and the unknown non-living component of the 1.3 x 10^4 MT C yr^{-1} consumed by suspension feeders. Much of the accumulation may occur as refractory material in the marshes and swamps and as fine organic matter associated with suspended or deposited sediments which never become available to estuarine decomposers. Sediment removal by dredging and loss to the ocean with bedload transport along the bottom, neither of which could be estimated, certainly would alter this estimate of detritus retention. More important, there are no estimates of the the fluxes of dissolved organic carbon (DOC) from estuarine primary producers, which can comprise a large contribution of organic carbon to the estuarine food web, either directly via DOC to microbes or indirectly via transformation to particulate organic carbon (POC) utilizable by metazoans (Baylor and Sutcliffe 1963, Riley 1963, Sieburth and Jensen 1968).

Aside from these first-order approximations of the quantity of detritus transported into and out of and generated within the estuary, the quality of the detritus is also a critical aspect of its contribution to the estuarine food web. "Quality" of detritus refers to its chemical lability and susceptibility to microbial and biological decomposition. This is important because, ultimately, the relative contribution of the respective detrital inputs and the subsequent losses as outputs to sediments of the North Pacific Ocean cannot be compared without considering the rate and efficiency at which detritus can be incorporated into the decomposer-grazer base of the estuarine food web.

9.1.5 Primary Consumers

Primary consumers in the estuary encompass a variety of taxa and sizes of organisms, from microscopic zooplankters to beavers. Dominant wetland consumers of emergent vascular plants were nutria, muskrat, and American beaver; other wetland herbivores such as dabbling ducks, deer, mice, voles, and insects were either comparatively unimportant or were not assessed. When found in the marsh and swamp habitats surrounding the peripheral bays, densities of wetland herbivores ranged narrowly between 14.2 and 15.5 animals ha^{-1}, realizing an estimated annual production of 0.12 to 0.15 gC m^{-2} yr^{-1} in these habitats. Total annual carbon production by wetland herbivorous mammals was estimated to be 6.78 MT C yr^{-1} and consumption was estimated to be between 380 and 3,028 MT C yr^{-1}.

Within the water column, suspension-feeding zooplankton were the predominant primary consumers of phytoplankton. Dominant planktonic zooplankton taxa included calanoid (predominantly *Eurytemora affinis*, *Pseudocalanus elongatus*, *Acartia clausi*, *Paracalanus parvus*, *Diaptomus ashlandi*) and cyclopoid (*Cyclops* spp.) copepods, cladocerans (*Bosmina longirostris*, *Daphnia* spp.), and rotifers. In the main channel through the Estuarine Channels and Fluvial Regions of the estuary, planktonic zooplankton density ranged between 560 and 14 X 10^4 organisms m^{-2} but prolonged, high concentrations of endemic estuarine zooplankton (particularly *E. affinis*) in the region of the turbidity maximum zone produced annual production estimates three times as high (21.7 gC m^{-2} yr^{-1}) as in the fluvial region (7.4 gC m^{-2} yr^{-1}). Using several assumptions, the total annual carbon production of suspension-feeding zooplankton was estimated to be approximately 0.3 x 10^4 MT C yr^{-1} and consumption approximately 0.1 x 10^4 MT C yr^{-1}.

Different assemblages of suspension- and deposit-feeding zooplankton occurred at the epibenthic interface between the water column and the bottom sediment surface. These assemblages were dominated by deposit-feeding harpacticoid copepods (principally *Scottolana canadensis*, one or more species of *Ectinosomidae*, *Microarthridion littorale*, and *Tachidius* spp.), by gammarid amphipods (*Corophium* spp. and *Eogammarus confervicolus*), and by ostracods (*Limnocythere* sp.). Suspension-feeding zooplankters such as *Eurytemora* or those imported from fluvial environs (e.g. rotifers, *Cyclops* spp., *Diaptomus* spp., *Bosmina* sp., *Daphnia* spp.) were also collected frequently within epibenthic habitats. These epibenthic zooplankton assemblages were estimated to produce approximately 65 MT C yr^{-1} and consume approximately 325 MT C yr^{-2}.

Deposit-feeding and suspension-feeding infauna, including *Corophium salmonis*, chironomid larvae, *Macoma balthica*, *Neanthes limnicola*, oligochaetes, *Corbicula manilensis*, *Mya arenaria*, among others, produced carbon at an estimated rate of 390 MT C yr^{-1} from consumption of 1,950 MT C yr^{-1}.

9.1.6 Predators

Predators or secondary and tertiary consumers include organisms which reside within the estuary for their entire life cycle as well as those which only sporadically occur in estuarine habitats. While densities of endemic predators such as demersal fish and macroinvertebrates appear to be relatively stable, suggesting some limiting levels of carrying capacity, more ephemeral predators such as schooling fishes and migratory birds often occur in high densities and, at such times, impose tremendous consumption pressures upon the available food resources. In some cases, such as some migratory fish, birds, and marine mammals, the estuary may serve only as a refuge during passage to other breeding and foraging environs.

Total predator production was estimated to be approximately 167 MT C yr^{-1}, resulting from consumption of approximately 0.2×10^4 MT C yr^{-1}.

9.2 THE RIVER-ESTUARY-PLUME CONTINUUM

The Columbia River Estuary is physically and biologically only part of a larger river-estuary-plume continuum. Conomos et al. (1972) divided the plume into a transitional area from the ends of the jetties to about 20 km offshore and an oceanic area seaward of the transition area. This division probably reflects accurately the strength in offshore areas of the biological, chemical, and geological influence of the river. The transitional area is characterized by strong spatial and temporal changes in water mass properties and moderate tidal currents which, although strong relative to those further offshore, are still weak relative to those within the estuary. Because of the very large river inflow to this estuary, many processes occur in the transition and even in the oceanic areas of the plume that normally occur inside other estuaries. In this regard, the Columbia River resembles systems such as the Congo River more than it resembles most other North American estuaries.

From a dynamic point of view, there is a relatively abrupt change between the estuarine processes that occur upriver of Jetty A (RM-3) and the coastal processes modified by the Columbia River plume observed seaward of the ends of the jetties. Estuarine circulation is highly energetic, dominated by the tides, strongly influenced by bottom friction, and essentially two-dimensional. Cross-channel variability becomes increasingly prominent as the system widens seaward of Clatsop Spit, but beyond the ends of the jetties the circulation of the plume can only be characterized as both time-dependent and fully three-dimensional. The force of the jet of tidal flow emerging from the estuary during ebb tide is quickly dissipated as the plume spreads, and the tides appear to be less important than the atmospherically-driven coastal circulation, even within the transition area. The only topographic constraint is the shoreline, and the movement of the plume is essentially independent of the bottom boundary because of the strong stratification at the base of the plume. The abrupt transition between estuarine and coastal circulation patterns is perhaps analogous to the discontinuity in primary production processes that occurs at the boundary between the tidal-fluvial and estuarine mixing zones of the estuary.

Conomos et al. (1972) argued that: (1) summer primary productivity is nutrient limited; (2) subsurface ocean water is brought close to the surface by coastal upwelling processes; (3) entrainment of subsurface ocean water within the transition area caused by the flow of the river plume over the coastal oceanic waters provides a nutrient source; and (4) there is an associated productivity maximum within the transition area. Further offshore, in the oceanic part of the plume, nutrients in the plume have been depleted, subsurface ocean water is not immediately below the plume to replenish nutrients, further mixing/entrainment occurs only with nutrient-poor surface ocean water, and productivity is low. Thus, the plume includes an offshore transition area of approximately 60,000 ha in which productivity of marine phytoplankton is potentially enhanced. This equals approximately 150% of the total surface area of the estuary between the mouth and RM-47.

Maximum productivity (on a mgC m^3 hr^{-1} basis) and chlorophyll a concentrations in the transition area are similar to those observed in the tidal-fluvial zone, but the photic depth is considerably deeper offshore, so total productivity within the transition area may be greater. Thus, presumably because of the high energy and large temporal variability in salinities, the estuary may represent an area of reduced primary productivity between the plume and tidal-fluvial areas of enhanced productivity (Frey and Small 1984). This pattern is typical of estuaries dominated by freshwater plankton and contrasts markedly with estuaries dominated by marine phytoplankton or "external" estuaries such as the Amazon and Chang Jiang (Yangtze) Rivers systems, where essentially all productivity occurs in the ocean.

However, at times the mid-estuary depression in primary productivity may be more than compensated for by the entrainment and increased availability of detritus in the region of the turbidity maximum. Such variability in the availability of phytoplankton and detrital carbon may explain the success of consumers such as *Eurytemora affinis*, which have the ability to exploit both food resources, to sustain high levels of production completely within the estuary.

9.3 CONSEQUENCES OF HISTORICAL CHANGES TO THE ECOSYSTEM

Over the past century, man and nature have wrought many changes to the Columbia River and its estuary. The more dramatic consequences of these changes are readily apparent in the physiography and habitat distribution of the estuary at present as compared to the period prior to regulation and diversion of the riverflow, diking and jetty construction in the estuary, and logging, agriculture, and other intensive land uses throughout the watershed and estuary. As Thomas (1983) indicated in his detailed documentation of changes in the estuary over this period, a net loss of over 142 km^2 (30% of the total surface area of the estuary) of shallows, flats, and tidal marshes and swamps can be attributed to diking and filling. And, as the result of a variety of anthropogenic and natural changes over the same period, there has been a net shift of approximately 45 km^2 (16%) of open water habitats to shallows and flats.

Determination of circulation characteristrics of the estuary in the late 1800's was accomplished by analyses of historical hydrologic and tidal data and the use of the laterally-averaged circulation model with the 1868 bathymetry. Results from the simulations of present and past circulation indicated that tidal transport has been reduced due to reduction of the tidal prism by 10% to 15%, and that blocking of subsidiary channels and subsequent confinement of the flow to the major channels has increased the cross-sectional area of the major channels. The ebb tidal flow has been redirected from the north channel to the south channel, altering the pattern of flow predominance. Salinity intrusion has been decreased and stratification increased despite increased sill depth at the entrance and reduced mean riverflow, because the tidal transport that is the primary agent of salt transport has been reduced. The increased minimum flows and the increased stratification have reduced maximum salinity intrusion into productive tidal flat and demersal slope habitats of Cathlamet Bay from more than 10 ppt to about 1 ppt. The neap-spring transition in stratification that presently allows maximum salinity intrusion on low-flow neap tides was more prominent at higher riverflows in 1868 than at present.

It is possible that neap-spring changes in water column primary and secondary productivity were more important in 1868 because neap-spring variations in the salinity structure were apparently more pronounced during the spring, high-productivity period. Changes in the tidal regime have altered turbidity maximum processes by channeling and redirecting the mean flow, increasing the residence time in peripheral channels and altering the neap-spring transitions in stratification. Peripheral areas are now more favorable for deposition because of reduced shear stress. However, our present lack of knowledge about high flow period turbidity maximum processes and the changes in neap-spring transitions render deductions about historic changes in these processes very difficult.

Overall, energy input to the estuary has been reduced and stabilized, i.e., the system has been physically tranquilized. Historical biological changes within the estuary are more complicated and difficult to hindcast, for there are neither ecosystem simulation models with which to examine historical scenerios nor pre-development biological data. Some effects are relatively obvious. Dramatic declines in some biotic resources such as Pacific salmon have been as obvious as the physical changes (Netboy 1974, Salo and Stober 1977) but, in the case of salmon, it is impossible to separate estuarine influences from those of overexploitation, loss of spawning habitat, declining water quality, blockages and hindrances to migration, and the many other external factors which have ultimately contributed to the demise of most of the Columbia River salmon stocks. The decreased salinity intrusion suggests the amount of habitat available for motile macroinvertebrates such as Dungeness crab and crangonid shrimp has been reduced. The distributions of these motile macroinvertebrates is evidently tied to euhaline and estuarine waters, respectively.

It is also likely that the reduced tidal prism has resulted in a reduction of the excursion zone of the turbidity maximum in the estuary. This would, in turn, imply that recycling and possibly sedimentation of fine particulates associated with the turbidity maximum may have occurred diffusely across a wider expanse of the estuary prior to 1885, instead of being concentrated below Tongue Point as it is now. However, the effects of decreased tidal energy in modern times must also be considered in relation to the concomitant reduction and smoothing of river discharge and the increased confinement of riverflow in the simplified channel network. Although there is now less tidal energy to resuspend sediments (promoting deposition), there may be a lower supply of sediments to the system. Nevertheless, deposition rates, especially in the peripheral bays and now inactive channels, are apparently now much higher. Another consideration is that periodically extreme river discharges (annual freshets and 100-yr or more cycle floods) occurred prior to regulation and partial diversion of riverflow. Floods may have transported more sediment into the estuary, both suspended sediment and bedload, but the high flows may also have flushed the estuary of recently-deposited sediments. This would suggest that fine-grained sedimentation is now more important (relative to bedload deposition) than historically. Another factor that must be considered is the influence of modern land use practices in promoting sediment discharge, but this cannot be evaluated in the absence of relevant historical data. Thus, although no data exists to evaluate sedimentation in the Columbia River Estuary prior to the arrival of man, it appears that the modern sedimentation rates are higher than pre-historic rates, and involve a higher fraction of fine sediments.

It is not possible to quantify changes in magnitudes and rates of production and consumption in the estuary, but the qualitative changes in physical processes can be related to the biotic community. Although compared with other estuaries around the world this estuary is still at the oligotrophic end of the scale, human influence is eutrophying the Columbia River Estuary. Riverine input of organic carbon has probably increased dramatically and the input of nutrients has decreased due to the increased phytoplankton production behind the dams on the lower reaches of the river. Local tributary inputs of particulates to peripheral bays have also probably increased. Estuarine flushing time and stratification have increased, but not to the extent of depleting dissolved oxygen in the main body of the estuary as has been well documented for more altered estuaries such as Chesapeake Bay (Officer et al. 1984). Further movement toward eutrophication should not be allowed, however, without a much better understanding of estuarine ecodynamics than we have today.

In summary, wetland and shoreline development and alteration of the estuary to meet the needs of navigation have resulted in documentable effects upon the morphology and circulation. Resultant effects upon biological processes in the estuarine ecosystem can be inferred but there is no direct data for quantitative evaluation. The effects of having altered the hydrologic regime are less clear because major alterations are very recent; certainly diversion of freshwater flow has and will continue to increase estuarine flushing time. The long-term trends are similar to those which have resulted in more serious problems in other, less energetic systems. That they have not yet reached the crisis point in the Columbia River Estuary is fortunate. It is imperative, however, that further development within both the estuary and the river basin be conducted with due regard to the long-term and cumulative impacts of the many small changes that have and will continue to occur.

9.4 GAPS IN UNDERSTANDING OF ECOSYSTEM AND RECOMMENDATIONS FOR FURTHER RESEARCH

Despite the complexity of estuarine interactions and the incomplete physical and biological data bases, results of the CREDDP studies have been integrated to the point that important ecosystem interactions such as the dynamics of salinity intrusion and its influence upon pelagic zooplankton, epibenthic fauna, and fishes have been partially elucidated. From this base of knowledge it is much easier to focus future research in directions which will, with efficient use of scientific energies and funds, provide a more complete and refined understanding of important ecological processes. In addition, further research in the estuary can logically be directed at processes which are identified as important to the evaluation of estuarine management decisions. The following sections describe our conclusions about the critical gaps revealed by the CREDDP studies and how these might be addressed.

9.4.1 Estuarine Circulation and Sedimentation

Undoubtedly one of the more important implications of the circulation and sedimentation studies was the critical role of the mid-estuary shoals (Desdemona and Taylor Sands) in the salt, mass, and sediment balance of the estuary. Although substantial exchanges of water, salt, and sediment are believed to occur in subsidiary channels that cross these shoals, the only data available to assess these transports is the sediment structure and these data cannot provide the necessary rate information. Both field experiments and modeling studies are needed to further evaluate the fluxes of water, salt, and sediment across the mid-estuary flats.

The Columbia River entrance has been a serious hazard to navigation for over a century and has also limited the collection of oceanographic data. Despite plans to deepen the entrance channel, knowledge of this area is inadequate for the modeling of estuarine processes, and for tidal current and severe wave predictions, channel design studies, or management of dredging. It is, for example, important to know whether critical conditions are reached at any stage of the tide for propagation of internal waves, because such hydraulic control at the entrance (or elsewhere) would affect circulation processes throughout the estuary. In addition, the sediment flux through the entrance is almost completely unknown. A program designed to analyze and model flow and transport through the entrance, and coupled with supporting physical measurements, is greatly needed.

The peripheral bays are another geographic area where physical characteristics and processes are inadequately known. Data of all kinds are lacking for Grays Bay and insufficient for the complex channel network of Cathlamet Bay and the islands of the tidal-fluvial zone. The bays are difficult to study either with moored instruments or profiling gear because they are shallow. Moreover, atmospheric effects are probably more important there, making any short segment of data more difficult to relate to the mean conditions. Our state of knowledge of the circulation in the main body of the estuary has now reached the point that sampling and modeling can be productively directed toward the peripheral bays, despite the difficulties of working in them.

Thorough understanding of the neap-spring transition in density structure and salt transport is inhibited by lack of critical data. For example, profile data are lacking during the high flow season and no acoustic echo sounding transects are available for any season. The acoustic records are probably the simplest and most useful data to obtain. They can provide qualitative information on the form and extent of salinity intrusion, vertical mixing, transport processes, etc. These records, combined with conductivity-temperature-depth (CTD) profiling, constitute a relatively inexpensive approach to determining the extent of salinity intrusion into peripheral bays and resolving the dependence of mixing on tidal range and riverflow.

Other recommended studies specific to the Columbia River Estuary include: (1) further refinement of the two-dimensional, laterally-averaged circulation model to calculate Lagrangian (particle drift) velocities and to better resolve mixing processes critical to the neap-spring transition; (2) quantitative assessment of the function, occurrence, and distribution of fronts; and (3) more detailed energy budget calculations with the one-dimensional model that would include the diurnal tides and the tidal overtones.

Finally, the strong influence of channel topography, the neap-spring variations, and the interaction between circulation, mixing processes, internal waves, and the horizontal and vertical density gradients (stongly variable in space and time) pose a challenge to theoretical physical oceanographers. An improved theory of circulation in shallow, energetic estuaries is badly needed if systems as complex and variable as the Columbia River Estuary are to be understood.

The most important problem regarding the sedimentology of the estuary concerns the sediment budget. None of the various studies performed to date have successfully determined the rate of sediment transport into or out of the estuary. The historical bathymetry investigations reported here are a first step toward a sediment budget for the estuary; further estimates of the amount of material moved during dredging and diking operations and more refined estimates of the river sediment supply are needed.

Further studies of the sedimentation processes are required to understand the patterns of sediment transport in the estuary. Two approaches to measurements of sediment flux in the estuary that have been used in the CREDDP studies are promising. The side-scan sonar data that has already been acquired would be of even greater value if supplemented by determination of transport rates associated with bedform migration. Intensive studies in selected areas would efficiently provide much-needed information on transport rates that could then be applied to the known bedform distributions and produce semi-quantitative estimates of the bedload sediment transport patterns in the estuary. Estimates of suspended sediment fluxes are more difficult, but, in light of the established importance of the turbidity maximum on sedimentation in the peripheral bays and the role of detritus in the ecosystem of the estuary, measurements of the turbidity maximum over all relevant time scales is mandated. Estimates of the lateral and vertical fluxes of suspended sediment should be included in the future studies.

Because of the difficulty in making synoptic field measurements of sediment tranports over the entire spectrum of time scales and over the appropriate space scales, the convergence and divergence of sediment transport is best approached with numerical modeling techniques. The improvements in the circulation models that have been made under the CREDDP program have brought us a step closer to the ability to predictively model sediment transport in the estuary. Further efforts to develop a physically-based numerical approach to the problem are needed. In the next few years, advances in this field have the best chance of allowing management and development decisions regarding sedimentation to be based on reliable predictions.

From a geological prespective, the Columbia River Estuary is very poorly understood. The geological evolution of the estuary through both historic and recent time can be fruitfully approached through a comprehensive program of sonar and seismic profiling, coring, and dating. Several geologic events, including the Spokane Floods that occurred near the end of the last ice age and the eruptions of Mt. St. Helens, Mt. Adams, and Mt. Hood are likely to be preserved in the geologic record of the estuary. An understanding of the evolution of the Columbia River estuary will aid in the prediction of modern perturbations to the natural system. In addition, such studies will provide information valuable in the interpretation of geologic phenomena that developed in similar dynamic environments elswhere.

9.4.2 Detritus Sources and Cycling

Comparison of detrital carbon imported and exported to and from the estuary with that generated and consumed within the estuary indicates that much of the major carbon inputs to higher trophic levels cannot be accounted for. Detailed work on the formation, transport, and decomposition of detritus within the estuary should be done, particularly relative to: (1) conversion of living freshwater phytoplankton to non-living detrital particles in the region of the turbidity maximum; (2) import of allochthonous DOC and generation of autochthonous DOC by estuarine autotrophs and the utilization and transformation (to POC) of both within the primary consumer levels of the detritus-based food web; (3) movement and decomposition of marsh detritus after autumnal die-off of marsh plants; (4) production and decomposition of fecal matter from invertebrates and vertebrates; (5) quantitative assessment of the retention of vascular plant detritus in the sediments; and (6) neap-spring and seasonal variations in the turbidity maximum process.

Overlap of a "phytoplankton sink", where living, chlorophyllous phytoplankton lyse and die, with high concentrations of suspended particles, detritivorous epibenthic, and pelagic zooplankton in the turbidity maximum zone indicates that the structure and dynamic character of this shifting region of the estuary are important to detritus import, transformation, and utilization within the estuary. The turbidity maximum zone has not been adequately described, either in terms of the physical processes creating it and determining its position in the estuary or in its effect in entraining and concentrating living and non-living food particles and primary consumers. That it varies significantly during the tidal month and that important consumers have life spans within this time frame suggest that secondary productivity may have significant variations on tidal-monthly time scales that cannot be resolved with available data.

9.4.3 Taxonomic Structure of Phytoplankton and Benthic Microalgae Assemblages

Unlike most of the consumer fauna, taxonomic structure of primary producer flora in the various regions and habitats of the estuary are little known. The taxa-specific sensitivity of estuarine autotrophs (at least the benthic microalgae, macroalgae, and emergent vascular plants) to physicochemical gradients through the estuary provide the means to more precisely define habitat structure and assess habitat changes. Phytoplankton species composition needs to be examined in detail along the axis of the estuary during all seasons, and particularly in the region of the turbidity maximum, in order to better identify the location and timing of the "phytoplankton sink" effect upon freshwater phytoplankton. Similarly, synoptic sampling and multivariate analyses of emergent vascular plant assemblages should be expanded in order to quantitatively verify the habitat types empirically delineated by Thomas (1983).

9.4.4 Primary Production Processes

Given the many variables which affect the metabolism and bioenergetics of plants and thus the estimation of net diel primary production, more complete analysis of plant metabolism is required of all three principal primary producer groups. Such documentation should include: (1) measurement of nitrate, nitrite, and ammonium ion concentration during the summer (presumed nutrient limitation) period, and the uptake of these nitrogen forms by the autotrophs; (2) measurement of nighttime respiration by phytoplankton and benthic algae and of phytoplankton respiration below the euphotic zone during the day; (3) quantification of DOC excretion (as a fraction of net production) by all autotrophs; (4) direct, short-term production and respiration measurements on emergent vascular plants; (5) patterns of deposition of planktonic diatoms in the estuary's littoral flats as related to circulation and sedimentation processes; and (6) neap to spring variability in productivity and fate of phytoplankton carbon.

9.4.5 Import and Export of Fluvial Phytoplankton and Zooplankton

Having illustrated the importance of fluvial phytoplankton and zooplankton import into the estuary from the Columbia River, there is an obvious need to better evaluate the seasonal dynamics of this dramatic influx of producers and consumers. Taxonomic structures of water column phytoplankton and zooplankton assemblages, primary production, and standing crop of phytoplankton and zooplankton need to be studied along a greater stretch of the Columbia River and Estuary. In particular, these measurements need to be made in the reservoirs behind the dams because these likely constitute areas of enhanced primary and secondary production which contribute significantly to estuarine production and detritus. Calculation of import and export can then be performed through the use of relatively simple box models, with transport parameters determined from riverflow and salinity data.

9.4.6 Consumption Processes

Although consumption was estimated using a number of tenuous assumptions about growth and production, the lack of complete primary consumption information was evident in many instances. This lack of data made it difficult to assess overall consumption of primary biomass in the estuary. In particular, grazing rate estimates are required for: (1) benthic infauna and epibenthic zooplankton feeding upon benthic microalgae and detritus; (2) freshwater and estuarine zooplankton feeding upon phytoplankton; and (3) herbivorous insects, birds, and wildlife (including small mammals such as mice and voles) feeding upon emergent vascular plants. The data on prey composition and consumption rates of secondary consumers is also deficient for many predator groups. Birds are the most obvious example. There is no direct indication of the types or amounts of food items consumed during their occupation of the estuary.

9.5 CONCLUSIONS

The Columbia River Estuary ecosystem is energetic and highly variable in both time and space. Circulation processes are driven by energy inputs from riverflow and the tides; the tidal energy is the dominant factor below Tongue Point. The variable energy input and non-linear interaction between topography, flow, mixing, and stratification produces a complex and variable circulation. Despite these complexities, circulation, sedimentation, and biological data all indicate that the system can be divided into three zones: tidal-fluvial, estuarine mixing, and plume and ocean. Because of the high energy level, very little fine sediment is permanently retained within the system. Fine sediments and detritus are, however, temporarily retained in the region of the turbidity maximum and peripheral bays. These accumulation zones have much longer residence times than the estuary as a whole. As a result of the energetic nature of the estuary, biological structure and processes are affected and limited more by the physical environment (e.g., turbidity, sediment stability) than by the ecological processes (e.g. predation) which structure less-energetic systems. In particular, the turbidity maximum appears to be a focal region of detritus accumulation and consumer production.

Although the geological history of the system is not well understood, it appears that riverflow regulation, shoreline development, and modifications for navigation have had the effects of reducing the tidal prism, altering circulation patterns, removing productive peripheral habitats, reducing and stabilizing riverflow, and increasing the sedimentation rate of fine sediments in the estuary. This sequence of events is qualitatively similar to that which has led to severe environmental degradation in less energetic estuaries. Therefore, future alterations of any component of the river-estuary-plume system should be based on thoughtful and systematic evaluation of long-term effects, a realization of the unity of the system, and a better understanding of the physical and biological processes and interactions than is available at the present time.

LITERATURE CITED
(Volume II)

Akins, G.J.; Jefferson, C.A. 1973. Coastal wetlands of Oregon. Natural Res. Invent. Rep. to Ore. Coastal Conserv. Dev. Comm. 159 pp.

Amspoker, M.C.; McIntire, C.D. 1978. Distribution of intertidal diatoms associated with sediment in Yaquina Estuary, Oregon. J. Phycol. 14:387-395.

Azam, F.; Fenchel, T.; Field, J.G.; Gray, J.S.; Meyer-Reil, L.A.; Thingstad, F. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. - Prog. Ser. 10:257-263.

Baylor, E.R.; Sutcliffe, W.H. Jr. 1963. Dissolved organic matter as a source of particulate food. Linnol. and Oceanogr. 4:369-371.

Biggs, R.B.; Flemer, D.A. 1972. The flux of particulate carbon in an estuary. Mar. Biol. 12:11-17.

Bottom, D.; Jones, K.K.; Herring, M.L. 1984. Fishes of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Bossanyi, J. 1957. A preliminary survey of the small natant fauna in the vicinity of the sea floor off Blyth, Northumberland. J. Anim. Ecol. 26:353-368.

Brett, J.R. 1979. Environmental factors and growth. Hoar, W.S.; Randall, D.J.; Brett, J.R. eds. Fish physiology, vol. VIII: Bioenergetics and growth, pp. 599-675. New York: Academic Press.

Bristow, M.P., Bundy, D.H.; Edmonds, C.M.; Ponto, P.E.; Frey, D.E.; Small, L.F. In prep. Airborne laser fluorosensor survey of the Columbia and Snake Rivers: simultaneous measurements of chlorophyll, dissolved organics and optical attenuation. Limnol. Oceanogr.

Brown, T.J.; Sibert, J.R. 1977. Food of some benthic harpacticoid copepods. J.Fish. Res. Board Can. 34:1028-1031.

Cadee, G.C.; Hegeman, J. 1977. Distribution of primary production of the benthic microflora and accumulation of organic matter on a tidal flat area, Balyzand, Dutch Wadden Sea. Neth. J. Sea. Res. 11:24-41.

Cardon, N.C. 1982. Effect of nutrient enrichment on marine benthic diatoms in Yaquina Bay, Oregon. Ph.D. thesis. Corvallis: Oregon State University.

Carefoot, T. 1977. Pacific seashores: A guide to intertidal ecology. Seattle, WA: Univ. Wash. Press. 208 pp.

Chervin, M.B. 1978. Assimilation of particulate organic carbon by estuarine and coastal copepods. Mar. Biol. 49:265-275.

Clairain, E.J.; Cole, R.A.; Diaz, R.J.; Ford, A.W.; Huffman, R.T.; Hunt, L.J.; Wells, B.R. 1978. Habitat development field investigations, Miller Sands marsh and upland habitat development site, Columbia River, Oregon. Tech. Rep. D-77-38, U.S. Army Corps Engineers Waterways Exp. Sta., Dredged Material Res. Prog., Vicksburg, MI. 78 pp. + append.

Claire, E.W., et al. 1971. The potential impact of severe water fluctuations on wildlife resources of the lower Columbia River. Spec. Rep. Ore. State Game Comm., Portland, OR.

Conomos, T.J.; Gross, M.G.; Barnes, C.A.; Richards, F.A. 1972. River-ocean nutrients relations in summer. Pruter, A.T.; Alverson, D.L. eds. The Columbia River Estuary and adjacent ocean waters, pp. 151-175. Seattle: University of Washington Press.

Craddock, D.R.; Blahm, T.H.; Parente, W.D. 1976. Occurrence and utilization of zooplankton by juvenile chinook salmon in the lower Columbia River. Trans. Am. Fish. Soc. 1:72-76.

Crawford, J.A.; Edwards, D.K. 1978. Postpropagation assessment of wildlife resources on dredged material. Clairain, E.J. ed. Habitat development field investigations, Miller Sands marsh and upland habitat development site, Columbia River, Oregon, Appendix F. Tech. Rep. D-77-38, Dredged Material Res. Prog., U.S. Army Corps Engineers Waterways Exp. Sta., Vicksburg, MI. 67 pp.

Crisp, D.J. 1971. Energy flow measurements. Holme, N.A.; McIntyre, A.D. eds. Methods for the study of marine benthos, pp. 197-279. Internat. Biol. Prog., Handbook 16. Oxford: Blackwell Sci. Pub.

Cushing, D.H. 1966. Models of the productive cycle in the sea. Morning Rev. Lect., Sec. Internat. Oceanogr. Conf., pp. 103-116. in Moscow: UNESCO.

Dame, R.F. 1976. Energy flow in an intertidal oyster population. Est. Mar. Sci. 4:243-253.

Davis, G.E.; Warren, C.E. 1971. Estimation of food consumption rates. Ricker, W.E. ed. Methods of assessment of fish production in fresh waters, pp. 227-248. IBPL Handbook 3. Oxford; Blackwell Sci. Pub.

Davis, J.S.; Holton, R.L. 1976. Diel activity of benthic crustaceans in the Columbia River Estuary. M.S. thesis. Corvallis: Ore. State Univ. 170 pp. + append.

Davis, M.W.; McIntire, C.D. 1983. Effects of physical gradients on the production dynamics of sediment-associated algae. Mar. Ecol. Prog. Serv. 13:103-114.

Davison, M.A. 1979a. Completion report: Columbian white-tailed deer literature review and study plan (unpubl.). Project E-2. Olympia: Washington Department of Game.

Davison, M.A. 1979b. Columbian white-tailed deer status and potential on off refuge habitat. Columbian White-tailed Deer Study Completion Rep., Proj. E-1. Olympia: Wash. Dept. Game.

Dawley, E.M.; Sims, C.W.; Ledgerwood, R.D. 1978. A study to define the migrational characteristics of chinook and coho salmon and steelhead trout in the Columbia River Estuary. Ann. Rep. 1977. Proj. 712, NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 23 pp. + append.

Dawley, E.M.; Sims, C.W. Ledgerwood, R.D.; Miller, D.R.; Thrower, F.P. 1979. A study to define the migrational characteristics of chinook and coho salmon and steelhead trout in the Columbia River Estuary. Ann. Rep. 1978, Proj. 712, NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 35 pp + append.

De Wilde, P.A.W.J. 1975. Influence of temperature on behavior, energy metabolism and growth of Macoma balthica. Barnes, H. ed. Proc. 9th European Mar. Biol. Symp., pp. 239-259. Aberdeen Univ. Press.

Dunn, J.; Hockman, G.; Howerton, J.; Tabor, J. 1984. Key mammals of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Durkin, J.T. 1973. A list of crustacean shellfish of the lower Columbia River between the mouth and river mile 108, July to October 1973. Unpubl. rep., NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 4 pp.

Durkin, J.T. 1974. A survey report of fish species found in a proposed fill area west of the Port of Astoria docks. Unpubl. rep., NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 5 pp.

Durkin, J.T. 1975. An investigation of fish and decapod shellfish found at four dredge material disposal sites and two dredge sites adjacent to the mouth of the Columbia River. Compl. Rep. to U.S. Army Corps Engineers Portland Dist., NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 29 pp.

Durkin, J.T. 1980. Columbia River Estuary finfish and shellfish utilization. Proc. 60th Ann. Conf. Western Assoc. Fish Wildl. Agen., July 13-17, 1980, Kalispell, Montana, pp. 334-342.

Durkin, J.T. 1982. Migration characteristics of coho salmon (Oncorhynchus kisutch) smolts in the Columbia River and its estuary. Kennedy, V.S. ed. Estuarine comparisons, pp. 365-376. New York: Academic Press, Inc.

Durkin, J.T.; Emmett, R.L. 1980. Benthic invertebrates, water quality, and substrate texture in Baker Bay, Youngs Bay, and adjacent areas of the Columbia River Estuary. Fin. Rep. to U.S. Fish Wildl. Serv., Ecol. Serv. Div., Coastal Zone Est. Studies, NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 44 pp. + append.

Durkin, J.T. Sims, C.W. 1975. Migrations of juvenile coho salmon, Oncorhynchus kisutch, into the Columbia River Estuary, 1966-71. Unpubl. rep., NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA.

Durkin, J.T.; Lipovsky, S.J.; Snyder, G.R.; Tuttle, M.E. 1977. Environmental studies of three Columbia River estuarine beaches. NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 68 pp.

Durkin, J.T.; Lipovsky, S.J.; McConnell, R.J. 1979a. Biological impact of a flowlane disposal project near Pillar Rock in the Columbia River Estuary. Final Rep. to U.S. Army Corps Engineers Portland Dist. NOAA, Natl, Mar. Fish. Serv., NW alaska Fish. Cntr., Coastal Zone Est. Studies Seattle, WA. 92 pp.

Durkin, J.T.; Lipovsky, S.J.; Snyder, G.R.; Shelton, J.M. 1979b. Changes in epibenthic estuarine fish and invertebrates from propeller agitation dredging. U.S. Army Corps Engineers, N. Pac. Div. Impact of propeller agitation dredging on fish and invertebrates at Chinook Channel in the Columbia River Estuary, Part II, Section I. Portland, OR. 57 pp.

Durkin, J.T.; Coley, T.C.; Verner, K.; Emmett, R.L. 1981. An aquatic species evaluation at four self-scouring sites in the Columbia River Estuary. Final Rep. to U.S. Army Corps Engineers. NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 46 pp.

Edwards, D.K. 1979. An analysis of avian communities on a dredged material island. M.S. thesis. Corvallis: Ore. State Univ. 48 pp.

Fauchald, K.; Jumars, P.A. 1979. The diet of worms: A study of polychaete feeding guilds. Oceanogr. Mar. Biol. Ann. Rev. 17:193-284.

Fenchel, T.M.; Jorgensen, B.B. 1977. Detritus food chains of aquatic ecosystems: the role of bacteria. Alexander M. ed. Advances in microbial ecology, vol. 1, pp. 1-58. New York: Plenum Press.

Fisher, T.R.; Carlson, P.R.; Barber, R.T. 1983. Carbon and nitrogen primary productivity in three North Carolina estuaries. Est. Coast. Shelf Sci. 15:621-644.

Fournier, R.O. 1966. Some implications of nutrient enrichment on different temporal stages of a phytoplankton community. Chesapeake Sci. 7: 11-19.

Frey, B.E.; Small, L.F.; Lara-Lara, R. 1984. Water column primary production in the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Frey, B.E.; Lara-Lara, J.R.; Small, L.F. In press. Reduced rates of primary production in the Columbia River Estuary following the May 18, 1980 eruption of Mt. Saint Helens. Est. and Coastal Res.

Furnas, M.J.; Hitchcock, G.L.; Smayda, T.J. 1976. Nutrient-phytoplankton relationships in Narragansett Bay during the 1974 summer bloom. Wiley, M.L. ed. Estuarine processes, vol. 1. New York: Academic Press.

Gallagher, J.L.; Daiber, F.C. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. Limnol. Oceanogr. 19:390-395.

Codin, J.-G.J. 1981. Effect of hunger on the daily pattern of feeding rates in juvenile pink salmon, *Oncorhynchus gorbuscha*. Walbaum. J. Fish. Biol. 19:63-71.

Goodin, J.-G.J. 1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can. J. Fish. Aquat. Sci. 38:10-15.

Good, J.W. 1977. Columbia River Estuary tidal marshes. Seaman, M.H. ed. Columbia River Estuary: inventory of physical, biological and cultural characteristics, pp. 1019. Astoria, OR: Columbia River Estuary Study Taskforce.

Greene, C.W. 1911. The migration of salmon in the Columbia River. Bull. U.S. Bur. Fish. 19:129-148.

Grontved, J. 1960. On the productivity of microbenthos and phytoplankton in some Danish fjords. Meddr. Danm. Fiskeri-og Havunders. N.S. 3:55-92.

Guillard, R.R.L.; Ryther, J.H. 1962. Studies of marine planktonic diatoms. Can. J. Microbiol. 8:229-239.

Haertel, L.S.; Osterberg, C.; Curl, H.; Park, P.K. 1969. Nutrient and plankton ecology of the Columbia River Estuary. Ecology 50:962-978.

Haertel, L.; Osterberg, C. 1967. Ecology of zooplankton, benthos and fishes in the Columbia River estuary. Ecology 48:459-472.

Haertel, L.S. 1970. Plankton and nutrient ecology of the Columbia River Estuary. Ph.D. thesis. Corvallis: Oregon State University.

Haney, J.F. 1973. An *in situ* examination of the grazing activities of natural zooplankton communities. Arch. Hydrobiol. 72:87-132.

Hazel, C.R.; Ives, J.H.; Miller, K.J.; Edwards, D.K.; Tinling, J.S.; Dorsey, G.L.; Green, M.; Crawford, J.A. 1984. Avifauna of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Healey, M.C. 1979. Detritus and juvenile salmon production in the Nanaimo Estuary: I. Production and feeding rates of juvenile chum salmon (Oncorhynchus keta). J.Fish. Res. Board Can. 36:488-496.

Heilman, P.E.; Greer, D.M.; Braun, S.E.; Baker, A.S. 1978. Postpropagation assessment of botanical and soil resources on dredged material. Habitat development field investigations, Miller Sands marsh and upland habitat development site, Columbia River, Oregon, Appendix E. Tech. Rep. D-77-38, Dredged Material Res. Prog., U.S. Army Corps Engineers Waterways Exp. Sta., Vicksburg, MI. 78 pp.

Heinle, D.R.; Flemer, D.A. 1975. Carbon requirements of a population of the estuarine copepod Eurytemora affinis. Mar. Biol. 31:235-247.

Heinle, D.R.; Harris, R.P.; Ustach, J.F.; Flemer, D.A. 1977. Detritus as food for estuarine copepods. Mar. Biol. 40:341-353.

Hempel, C. 1957a. ....Kieler Meersforsch. 13:275-288.

Hempel, C. 1957b. ....Helgolander wiss. Meeresunters. 6:100-135.

Hesthagen, I. 1973. Diurnal and seasonal variations in the near-bottom fauna - the hyperbenthos - in one of the deeper channels of the Kieler Bucht (western Baltic). Kieler Meeresforsch. 29:116-140.

Higley, D.L.; Holton, R.L. 1975. Biological baseline data: Youngs Bay, Oregon 1974. Fin. Rep. to Alumax Pac. Alumin. Corp., Ocean. ref. 75-6, School Ocean., Ore. State Univ., Corvallis, OR. 91 pp.

Higley, D.L.; Holton, R.L. 1978. A grab-sample study of the benthic invertebrates of the Columbia River Estuary. Suppl. Data Rep. to Ocean. Ref. 76-3, School Ocean., Ore. State Univ., Corvallis, OR. 27 pp.

Higley, D.L.; Holton, R.L. 1979. Biological baseline and fluoride effects data for Youngs Bay, Oregon, 1974-1975. Corvallis: School Ocean., Ore. State Univ. 91 pp.

Higley, D.L.; Holton, R.L.; Komar, P.D. 1976. Analysis of benthic infauna communities and sedimentation patterns of a proposed fill site and nearby regions in the Columbia River Estuary. Corvallis: School Ocean., Ore. State Univ. 78 pp.

Hirose, P. 1977. Incidence of seal-damaged salmonids sampled from the lower Columbia River gill-net fishery, 1972-1976. Info. Rep. 77-4. Portland: Ore. Dept. Fish Wildl. 6 pp.

Holton, R.L.; Higley, D.L. 1976. Gammaridean amphipods in the Columbia River Estuary, Proc. 5th Tech. Conf. Est. in the Pac. Northwest, pp. 9-12. Circ. 51, Engineering exp. Sta. Corvallis: Ore. State Univ.

Holton, R.L.; Higley, D.L.; Brzezinski, M.A.; Jones, K.K.; Wilson, S.L. 1984. Benthic infauna of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Inman, D.L. 1952. Measures for describing the size distribution of sediments. J. Sediment. Petrology 22:125-145.

Ives, F.; Saltzman, W. 1970. A special report to the State Department of Transportation. Portland: Ore. State Game Comm. 17 pp.

Jeffries, S.J.; Treacy, S.D.; Geiger, A.C. 1984. Marine mammals of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Johnsen, R.C.; Sims, C.W. 1973. Purse seining for juvenile salmon and trout in the Columbia River Estuary. Trans. Am. Fish. Soc. 102:341-345.

Johnson, M.L.; Jefferies, S.J. 1977. Population evaluation of the harbor seal (*Phoca vitulina richardsi*) in the waters of the State of Washington. Rep. to U.S. Marine Mammal Comm., Contract MM5AC019. Tacoma, WA: Univ. Puget Sound. 27 pp.

Jones, K.K.; Bottom D.L.; 1984. Zooplankton and larval fishes of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Jonge, V.N. de. 1980. Fluctuation in the organic carbon to chlorophyll *a* ratios for estuarine benthic diatom populations. Mar. Ecol. Prog. Ser. 2:345-353.

Jorgensen, B.B. 1977. The sulfur cycle of a coastal marine sediment (Limfjorden, Denmark). Limnol. Oceanogr. 22:814-832.

Jumars, P.A.; Self, R.F.L.; Nowell, A.R.M. 1982. Mechanics of particle selection by tentaculate deposit-feeders. J. Exp. Mar. Biol. Ecol. 64:47-70.

Kistritz, R.U.; Hall, K.J.; Yesaki, I. 1983. Productivity, detritus flux, and nutrient cycling in a *Carex lyngbyei* tidal marsh. Estuaries 6:227-236.

Kitchell, J.F.; Stewart, D.J.; Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedian vitreum vitreum*). J. Fish. Res. Board Can. 34:1922-1935.

Klir, G.J. 1969. An approach to general systems theory. Princeton, NJ: Van Nostrand-Reinhold.

Kremer, J.N.; Nixon, S.W. 1978. A coastal marine ecosystem; simulation and analysis. New York: Springer-Verlag.

Kuipers, B.R.; Dapper, R. 1981. Production of Crangon crangon in the tidal zone of the Dutch Wadden Sea. Neatherlands J. Sea Res. 15:33-53.

Lara-Lara, J.R. 1983. Primary biomass and production processes in the Columbia River Estuary. Ph.D. thesis. Corvallis: Oregon State University.

Lasker, R. 1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. Steele, J.H. ed. Marine food chains pp. 265-284. Berkeley, CA: Univ. Calif. Press.

Leach, H.J. 1970. Epibenthic algal production in an intertidal mudflat. Limnol. Oceanogr. 15:514-521.

LeBrasseur, R.J. 1969. Growth of juvenile chum salmon (Oncorhynchus keta) under different feeding regimes. J. Fish. Res. Board Can. 26:1631-1645.

Lindeman, R.L. 1941. Seasonal food-cycle dynamics in a senescent lake. Amer. Midl. Nat. 26:636-673.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399-418.

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

Mann, K.H. 1969. The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6:1-81.

Mann, K.H. 1982. Ecology of coastal waters: A systems approach. Stud. Ecol. 8. Oxford: Blackwell Sci. Pub. 322 pp.

Marshall, N.; Oviatt, C.A.; Skauen, D.M. 1971. Productivity of the benthic microflora of shoal estuarine environments in southern New England. Int. Revue Ges. Hydrobiol. 56:974-956.

Marshall, S.M.; Orr, A.P. 1962. Food and feeding in copepods. Rapp. Cons. Explor. Mer. 153:92-98.

Maser, C.; Storm, R.M. 1970. A key to the Microtinae of the Pacific Northwest. Corvallis: Ore. State Univ. Bookstores.

Mate, B.R. 1975. Annual migrations of the sea lions Eumetopias jubatas and Zalophus californianus along the Oregon coast. Reapp. P.-v. Reun. Cons. Int. Explor. Mer. 169:455-461.

McAlister, W.B. 1981. Estimates of fish consumption by marine mammals in the eastern Bering Sea and Aleutian Island area. Unpubl. rep, NOAA, Natl. Mar. Mamm. Lab., NW Alaska Fish. Cntr., Seattle, WA.

McConnell, R.J.; Lipovsky, S.J.; Misitano, D.A.; Craddock. D.R.; Hughes, J.R. 1978. Inventory and assessment of predisposal and postdisposal aquatic habitats. Clairain, E.J. ed. Habitat development field investigations, Miller Sands marsh and upland habitat development site, Columbia River, Oregon, Appendix B. Tech. Rep. D-77-38, U.S. Army Corps Engineers Waterway Exp. Sta., Dredged Material Res. Prog., Vicksburg, MI.

McConnell, R.; Blahm, T.; McCabe, G. Jr.; Clocksin, T.; Coley, T.; Durkin, J.; Emmett, R.; Muir, W. 1983. Draft report: Salmonid and non-salmonid fish. Astoria, OR: Columbia River Estuary Data Development Program.

McIntire, C.D. 1973. Diatom associations in Yaquina Estuary, Oregon: a multivariate analysis. J. Phycol. 9:254-259.

McIntire, C.D. 1983. A conceptual framework for process studies in lotic ecosystems. In Fontaine T.D.; Bartell, J.M. eds. Dynamics of lotic ecosystems, pp. 43-68. Ann Arbor: Ann Arbor Science Publishers.

McIntire, C.D.; Amspoker, M.C. 1984. Benthic primary production in the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

McKern, J.L. 1976. Inventory of riparian habitats and associated wildlife along the Columbia and Snake Rivers, vol. I. Rep. to U.S. Army Corps of Engineers, North Pacific Division, Portland, OR.

McMahon, E. et al. 1974. A survey of great blue heron rookeries on the Oregon coast: a student-originated studies project. Charleston: Ore. Inst. Mar. Biol. 143 pp.

McNeill, S.; Lawton. J.H. 1970. Annual production and respiration in animal populations. Nature 225:472-474.

McQueen, D.J. 1970. Grazing rates and food selection in Diaptomus oregonensis (Copepoda) from Marion Lake, British Columbia. J. Fish. Res. Bd. Canada 27:13-20.

Merker, C.; Fenton, G. 1984. Key mammals of the Columbia River Estuary - density, food consumption, and limiting factors. Astoria, OR: Columbia River Estuary Data Development Program.

Miller, C.B. 1983. The zooplankton of estuaries. Ketchum, B.H. ed. Estuaries and enclosed seas, pp. 103-149. Amsterdam: Elsevier Sci. Pub. Co.

Miller, R.J.; Mann, K.H. 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. Mar. Biol. 18:99-114.

Misitano, D.A. 1974. Zooplankton, water temperature and salinities in the Columbia River Estuary, December 1971 through December 1972. Data Rpt. 92, U.S. National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Misitano, D.A. 1977. Species composition and relative abundance of larval and post-larval fishes in the Columbia River Estuary. 1973. Fish. Bull. 74:218-222.

Nakashima, B.S.; Leggett, W.C. 1978. Daily ration of yellow perch (Perca flavescens) from Lake Memphremagog, Quebec-Vermont, with a comparison of methods for in situ determinations. J. Fish. Res. Board Can. 35:1597-1603.

Nauwerck, A. 1959. Zur Bestimmung der Filtrierrate limnischer Planktontiere. Arch. Hydrobiol. (Suppl. 25) 1:83-101.

Nauwerck, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. Symbolae Botan. Upsalienses 17:1-163.

Netboy, A. 1974. The salmon: their fight for survival. Boston, MA: Houghton Miflin. 613 pp.

Officer, C.B. 1980. Box models revisited. Estuarine and wetland processes, pp. 65-114. New York: Plenum Press.

O'Reilly, J.E.; Thomas, J.P.; Evans, C. 1976. Annual primary production (nanoplankton, netplankton, dissolved organic matter) in the lower New York Bay. McKeon, W.H.; Lauer, G.J. eds. Fourth Symposium on Hudson River Ecology. New York: Hudson River Environmental Society, Inc.

Overton, W.S. 1972. Toward a general model structure for a forest ecosystem. Franklin, J.F.; Dempster, L.J.; Waring, R.H. eds. Proceedings of the symposium on research on coniferous forest ecosystems, pp. 37-47. Portland: Pacific Northwest Forest and Range Experiment Station.

Overton, W.S. 1975. The ecosystem modeling approach in the coniferous forest biome. Patten, B.C. ed. Systems analysis and simulation in ecology, Vol. III, pp. 117-138. New York: Academic Press, Inc.

Overton, W.S. 1977. A strategy of model construction. Hall, C.A.S.; Day, J.W. Jr. eds. Ecosystem modeling in theory and practice: an introduction with case histories, pp. 50-73. New York: John Wiley & Sons, Inc.

Pamatmat, M.M. 1968. Ecology and metabolism of a benthic community on an intertidal sandflat. Int. Revue Ges. Hydrobiol. 53:211-298.

Park, P.K.; Osterberg, C.L.; Forster, W.O. 1972. Chemical budget of the Columbia River. Pruter, A.T.; Alverson, D.L. eds. The Columbia River Estuary and adjacent ocean waters, pp. 123-134. Seattle: Univ. Wash. Press.

Parsons, T.R.; LeBrasseur, R.J. 1970. The availability of food to different trophic levels in the marine food web. Steele, J.H. ed. Marine food chains, pp. 325-343. Berkeley: Univ. California Press.

Parsons, T.R.; LeBrasseur, R.J.; Barraclough, W.E. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: a review. J. Fish. Res. Bd. Canada 27:1251-1264.

Parsons, T.R.; Takahashi, M. 1973. Biological oceanographic processes. New York: Pergamon Press.

Parsons, T.R.; Takahashi, M.; Hargrave, B. 1977. Biological oceanographic processes, 2nd ed. New York: Pergamon Press.

Pearson, J.P.; Verts, B.J. 1970. Abundance and distribution of harbor seals and northern sea lions in Oregon. Murrelet 51:1-5.

Pimentel, R.A. 1979. Morphometrics. Dubuque, Iowa: Kendall/Hunt Publishing Company. 276 pp.

Pinkas, L.; Oliphant, M.S.; Iverson, I.L.K. 1971. Food habits of albacore, bluefin tuna, and bonito in California water. Calif. Fish Game, Fish Bull. 152:1-105.

Platt, T. 1975. Analysis of the importance of spatial and temporal heterogeneity in the estimation of the annual production by phytoplankton in a small, enriched marine basin. J. exp. mar. Biol. Ecol. 18:99-109.

Platt, T.; Conover, R.J. 1971. Variability and its effects on the chlorophyll budget of a small marine basin. Mar. Biol. 10:52-65.

Pomeroy, L.R. 1959. Algal productivity in salt marshes of Georgia. Limnol. Oceanogr. 4:386-397.

Poulet, S.A. 1976. Feeding of Pseudocalanus minutus on living and non-living particles. Mar. Biol. 34:117-125.

Proctor, C.M.; Garcia, J.C.; Galvin, D.V.; Joyner, T.; Lewis, G.B.; Loehr, L.C.; Mass, A.M. 1980. An ecological characterization of the Pacific Northwest coastal region, Volume 1, Conceptual model. U.S. Fish and Wildlife Service, Biological Services Program FWS/085-79/11.

Raymont, J.E.G. 1980. Plankton and productivity in the oceans. New York: Pergamon Press.

Redfield, A.C.; Ketchum, B.H.; Richards, F.A. 1963. The influence of organisms on the composition of sea water. Hill, M.N. ed. The sea, vol. 2, pp. 26-77. London: Wiley-Interscience.

Reiper, M. 1978. Bacteria as food for marine harpacticoid copepods. Mar. Biol. 45:337-345.

Richman, S. 1958. The transformation of energy by Daphnia pulex. Ecol. Monogr. 28:273-291.

Riley, G.A. 1963. Organic aggregates in seawater and the dynamics of their formation and utilization. Limnol. and Oceanogr. 8:372-381.

Riznyk, R.Z.; Phinney, H.K. 1972. Manometric assessment of intertidal microalgal production in two estuarine sediments. Oecologia 10:193-203.

Rowe, K.; Brenne, R. 1981. Statistical interactive programming system (SIPS). Statistical Computing Rpt. 7. Corvallis: Oregon State University.

Salo, E.O.; Stober, Q.J. 1977. Man's impact on the Columbia River stocks of salmon. Proceedings of the conference assessing effects of power plant-induced mortality on fish populations, pp. 36-45. New York: Pergamon Press.

Scheffer, T.H. 1925. Notes on the breeding of beavers. J. Mammal. 6:129-130.

Seaman, M.H. ed. 1977. Columbia River Estuary: Inventory of physical, biological and cultural characteristics. Astoria, OR: Col. Riv. Est. Study Taskforce. 302 pp.

Sherwood, C.R.; Creager, J.S.; Roy, E.H.; Gelfenbaum, G.; Dempsey, T. 1984. Sedimentary processes and environments in the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Sibert, J. 1981. Intertidal hyperbenthic populations in the Nanaimo estuary. Mar. Biol. 64:259-265.

Siburth, J. McN.; Jensen, A. 1968. Studies on algal substances in the sea; I. Gelbstoff (humic material) in terrestrial and marine waters. J. Exptl. Mar. Biol. Ecol. 2:174-189.

Simenstad, C.A.; Miller, B.S.; Nyblade, C.F.; Thornburgh, K.; Bledsoe, L.J. 1979. Food web relationships of northern Puget Sound and the Strait of Juan de Fuca: A synthesis of available knowledge. EPA DOC Res. Rep. EPA-600/7-79-259. 335 pp.

Simenstad, C.A. 1984. Epibenthic organisms of the Columbia River Estuary. Astoria, OR: Columbia River Estuary Data Development Program.

Simenstad, C.A. In press. The ecology of estuarine channels of the Pacific Northwest: A community profile. U.S. Fish Wildl. Serv., Biol. Serv. Prog., Washington, D.C. FWS/OBS-83/05. 182 pp.

Simenstad, C.A.; Armstrong, D.A. In prep. The ecology of littoral flats of the Pacific Northwest coast: A community profile. U.S. Fish Wildl. Serv., Biol. Serv. Prog., Washington, D.C. FWS/OBS-84/__.

Sims, C.W. 1970. Juvenile salmon and steelhead in the Columbia River Estuary. Proc. NW Est. Coastal Zone Symp., pp. 80-86. Portland, OR: U.S. Dept. Interior, Bur. Sport Fish. Wildl.

Sims, C.W. 1974. Food of chum salmon fry in brackish and freshwater areas of the Columbia River Estuary. Unpubl. rep., NOAA, Natl. Mar. Fish. Serv., NW Alaska Fish. Cntr., Seattle, WA. 15 pp.

Small, L.F.; Curl, H.C.; Glooschenko, W.A. 1972a. Estimates of primary production off Oregon using an improved chlorophyll-light technique. J. Fish. Res. Bd. Canada 29:1261-1267.

Small, L.F.; Curl, H.C.; Glooschenko, W.A. 1972b. Effects of solar radiation and upwelling on daily primary production off Oregon. J. Fish. Res. Bd. Canada 29:1269-1275.

Smalley, A.E. 1958. The role of two invertebrate populations _Littorina irrorata_ and _Orchelimum fidicinum_ in the energy flow of a salt marsh ecosystem. Ph.D. thesis. University of Georgia. Athens: 126 pp.

Steele, J.H.; Baird, I.E. 1968. Production ecology of a sandy beach. Limnol. Oceanogr. 13:14-25.

Steele, J.H. (ed.) 1974. The structure of marine ecosystems. Cambridge, MA: Harvard Univ. Press.

Strickland, J.D.H. 1960. Measuring the production of marine phytoplankton. Fish. Res. Bd. Canada Bull. 122.

Strickland, J.D.H.; Parsons, T.R. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada Bull. 167. Ottawa: Queen's Printer.

Stross, R.G.; Stottlemeyer, J.R. 1965. Primary production in the Patuxent River. Chesapeake Sci. 6:126-140.

Suring, L.H.; Vohs, P.A. Jr. 1979. Habitat use by Columbian white-tailed deer. J. Wildl. Mgmt. 43:610-619.

Tabor, J.E. 1974. Productivity, survival, and population status of river otter in western Oregon. M.S. thesis. Corvallis: Ore. State Univ. 62 pp.

Tabor, J.E. 1976a. Vertebrate wildlife of the Skipanon River site. Montague-Bierly and Assoc. Natural resource base and physical characteristics of the proposed offshore oil platform fabrication site. pp. 23-63. Portland, OR.

Tabor, J.E. 1976b. Inventory of riparian habitats and associated wildlife along the Columbia and Snake Rivers, vol. 11A and 11B, lower Columbia River. Rep. to U.S. Army Corps Engineers, North Pacific Division. Corvallis: Coop. Wildl. Fish. Unit, Ore. State Univ. 861 pp.

Taghon, G.L.; Self, R.F.L.; Jumars, P.A. 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. Science 210:262-264.

Taguchi, S.; Fukuchi, M. 1975. Filtration rate of zooplankton community during spring bloom in Akkeshi Bay. J. Exp. Mar. Biol. Ecol. 19:102-116.

Tait, R.V. 1972. Elements of marine ecology. 2nd ed. London: Butterworths. 314 pp.

Tenore, K.R.; Dunstan, W.M. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. Mar. Biol. 21:190-195.

Tenore, K.R.; Goldman, J.C.; Clarner, J.P. 1973. The food chain dynamics of the oyster, clam, and mussel. J. Exp. Mar. Biol. Ecol. 12:157-165.

Thomas, D.W. 1983. Changes in Columbia River Estuary habitat types over the past century. Astoria, OR: Columbia River Estuary Data Development Program.

Thomas, D.W. In press. The vascular flora of the Columbia River Estuary. Wassmann Journal of Biology.

Thompson, K.; Snow, D. 1974. Fish and wildlife resources, Oregon coastal zone. Salem: Ore. Coastal Conserv. Dev. Comm. 114 pp.

Thorpe, J.E. 1977. Daily ration of adult perch, Perca fluviatilis L. during summer in Loch Leven, Scotland. J. Fish. Biol. 11:55-68.

Toweill, D.E. 1974. Winter food habits of river otters in western Oregon. J. Wildl. Mgmt. 38:107-111.

U.S. Army Corps of Engineers Portland District. 1972. Lower Columbia River bank protection project, Oregon and Washington - final environmental impact statement. Portland, OR. 50 pp.

U.S. Army Corps of Engineers Portland District. 1975. Columbia and lower Willamette River maintenance and completion of the 40-foot navigation channel downstream of Vancouver, Washington, and Portland, Oregon - environmental impact statement. Portland, OR. 77 pp.

U.S. Army Corps of Engineers Portland District. 1976. Lower Columbia River bank protection project, Oregon and Washington - final environmental impact statement. Supplement. Portland, OR. 170 pp.

U.S. Fish and Wildife Service. 1977. Columbian white-tailed deer recovery plan. U.S. Fish Wildlife Serv., Columbian White-tailed Deer Recovery Team.

Washington Department of Game. 1975. Marine shoreline fauna of Washington: A status survey. Coastal Zone Environ. Studies Rep. 1. Olympia, WA. 594 pp.

Werschkal, D.; McMahon, E.; Leitschuh, M.; English, S.; Skibinski, C.; Williamson, G. 1977. Observations on the reproductive ecology of the great blue heron (*Ardea herodias*) in western Oregon. Murrelet 58:7-12.

Westerheim, S.J. 1955. Migrations of starry flounder (*Platichthys stellatus*) tagged in the Columbia River. Ore. Fish Comm. Res. Briefs 6:33-37.

Williams, L.G. 1964. Possible ralationships between plankton-diatom species numbers and water-quality estimates. Ecology 45:809-823.

Williams, L.G. 1972. Plankton diatom species biomasses and the quality of American rivers and the Great Lakes. Ecology 53:1038-1050.

Wood, E.J.F.; Corcoran, E.F. 1966. Diurnal variation in phytoplankton. Bull. Mar. Sci. 16:383-403.

Woodward-Clyde Consultants. 1978. Inventory assessment of postpropagation terrestrial resources on dredged material. Clairain, E.J. ed. Habitat development field investigations, Miller Sands marsh and upland habitat development site, Columbia River, Oregon, Appendix C. Tech. Rep. D-77-38, Dredged Material Res. Prog. U.S. Army Corps Engineers Waterways Exp. Sta., Vicksburg, MI.

Yentsch, C.S.; Scagel, R.F. 1958. Diurnal study of phytoplankton pigments: an *in situ* study in East Sound, Washington. J. Mar. Res. 17:567-583.