FWS/OBS-83/05
December 1983

THE ECOLOGY OF ESTUARINE CHANNELS OF THE PACIFIC NORTHWEST COAST:
A Community Profile

Fish and Wildlife Service

U.S. Department of the Interior

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THE ECOLOGY OF ESTUARINE CHANNELS OF THE PACIFIC NORTHWEST COAST: A COMMUNITY PROFILE

by

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Prepared for

National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

Library of Congress Card No. 83-600586

This report should be cited as:

Simenstad, C.A. 1983. The ecology of estuarine channels of the Pacific Northwest coast: a community profile. U.S. Fish Wildl. Serv. FWS/OBS-83/05. 181 pp.

PREFACE

This profile of the estuarine channel habitats of the Pacific Northwest is one in a series of community profiles synthesizing information pertinent to specific habitats of particular interest to environmental managers. The intent of the series is to provide scientific information in a format that is useful to a broad spectrum of users including environmental managers, college educators, and interested laypersons. This specific profile focuses on the complex network of channels of various origins in the estuarine reaches of the coastal waters of the Pacific Northwest. The geographic scope or study area is primarily that region of the coast from Strait of Juan de Fuca on the north to Cape Mendocino, California, on the south.

In order to explain the ecology within these channel systems and their ecological relationships to the adjacent habitats or subecosystems, considerable effort was dedicated to detailing hydrological, geomorphological, and chemical components and processes of the systems as well as the biological. These factors in concert with the biota dictate both the short- and long-term ecological structure and function of these habitats. The final chapter integrates the information in the preceding chapters by detailing considerations for management.

Any questions or comments about or requests for publications should be directed to:

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CONVERSION FACTORS

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (mt)	2205.0	pounds
metric tons (mt)	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	1.8(C°) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
BTU	0.2520	kilocalories
Fahrenheit degrees	0.5556(F° - 32)	Celsius degrees

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ACKNOWLEDGMENTS

This synthesis of information on estuarine channels of the Pacific Northwest would have been virtually impossible without the aid and assistance of many individuals, to whom I extend my utmost gratitude. John Cooper, Jay Watson, Nancy Nelson, and their colleagues in the U.S. Fish and Wildlife Service were responsible for initiating and sustaining the effort, providing reference material, and generating critical reviews. Robert Holton and Duane Higley (Oregon State University, Corvallis), David Levy (Westwater Research Centre, Vancouver, B.C.), Colin Levings (Department of the Environment, Vancouver, B.C.), Ed Roy (University of Washington, Seattle), Dennis Paulson (University of Washington, Seattle), and Rocky Beach (Oregon Department of Fish and Wildlife, Astoria) all contributed data, reports, ideas, and review comments which were the crux of this synthesis. Independent reviewers who also provided extremely constructive comments included Alyn Duxbury (University of Washington, Seattle), Tom Gaumer (Oregon Department of Fish and Wildlife, Newport), and Charles Miller (Oregon State University, Corvallis). The incredibly fine illustrations were prepared by Cathy Eaton Walker of Friday Harbor, Washington. Appreciation is extended to Dr. Dennis Willows, Director of the University of Washington's Friday Harbor Laboratories, for the opportunity to obtain original aerial photographs of estuarine channels in Puget Sound. I am also grateful for the photographs provided by Rocky Beach, Dave Levy, and Dennis Paulson.

CHAPTER 1

INTRODUCTION[1]

1.1 OBJECTIVES

An estuary is a true interface, because it provides the aquatic boundary between riverine and marine ecosystems and because it is the principal source of interaction between man and the sea. Sediments, nutrients, biota, and commerce mutually flow among the terrestrial, riverine, and marine habitats via the estuary, with the majority of these interactions occurring within the channels which form the estuary's circulatory system. The importance of estuaries to navigation, transportation, and exploitation of food organisms has been appreciated by man for centuries, with a consequentially long history of uses and abuses. Unfortunately, the scientific knowledge about and public appreciation for the ecological role of estuaries is a recent and still-developing phenomenon. Long before the relationships between these alterations and the structure and production of estuarine biota were considered, however, estuarine channels became readily-available conduits for industrial effluents and domestic wastes. And perhaps even earlier, adjacent tideflats and wetlands were claimed for agriculture, industry, and colonization which resulted in major modification of channels through diking and filling. In general, it wasn't until effects upon human health and fisheries became obvious in the most heavily-impacted estuaries that such ecological relationships entered into the management of estuaries.

Although perhaps not as heavily utilized as other (e.g., east coast) estuaries, Pacific Northwest coast estuaries have been utilized extensively for log and lumber transport, storage and processing; harvest, culture, and processing of finfish and shellfish; dredging, filling, and diking; and industrial and urban waste disposal with little acknowledgment or knowledge of the role estuaries play in maintenance and production of fish and wildlife. Although much of the more direct, deleterious impacts have been mitigated in cases where commercially or otherwise important species have been overtly threatened, protection and management of estuaries has still not been approached on a scale of the ecosystem or its higher level components--communities or habitats.

It is being recognized, however, that effective management of coastal ecosystems is best accomplished at the level of the community or habitat (Gosselink et al. 1979), rather than at the species or taxa level. It is only at the community level that ecological relationships among biotic and abiotic components can be interpreted in terms of the functional processes which effect the dynamics of the system's structure and production. Thus, the role of riverine inputs, estuarine circulation, salinity gradients, nutrient and material fluxes, and sediment structure in determining the composition, distribution, and standing stock of estuarine biota can be translated into management recommendations for the maintenance of key processes. It is the extended inhibition of these key processes, rather than short-term perturbation of species populations, which will ultimately determine the resilience of the ecosystem and its component communities and habitats to natural and man-induced alterations.

---

[1] See the Glossary of Terms, Appendix A, for definition of terms utilized in the following text.

This document has been prepared with the objective of providing estuarine resource managers with a synopsis of the existing knowledge about the ecology of estuarine channels in the Pacific Northwest. Incorporated into this profile is a summary of the principal physical, chemical environments and biological features of channel communities, as well as an interpretive synthesis of the internal dynamics of the community and its relationships with other communities in the aggregate estuarine ecosystem.

And, while this community profile has been specifically prepared to provide information for the assessment, planning and permitting activities of the U.S. Fish and Wildlife Service, it will hopefully constitute an educational source document for all those interested in the ecological value of estuaries.

1.2 SCOPE

The region of geographic coverage (Fig. 1.1) is the Columbian Province (Cowardin et al. 1979), including the Northwest Pacific Coast from Cape Mendocino, California, to the Strait of Juan de Fuca on the Washington-Canada border. This embraces coastal estuaries as well as the continuum of estuaries forming the inland seas of Puget Sound and the southern Strait of Georgia, with the latter terminating between Vancouver on the mainland and Nanaimo on Vancouver Island.

Estuarine channel habitats are defined as incised subtidal estuarine bottoms or depressions which contain saline (≥ 0.05°/oo) water masses freely exchanged through tidal and riverine currents. This definition is intended to encompass both the principal corridor of water movement through the estuary, typically along its main longitudinal axis, as well as the complex dendritic or anastomosing drainages which dissect tideflats and saltmarshes.

The biotic community characterizing estuarine channels involves the micro- and macroflora and fauna found, whether resident or transitional, in or on the water column or subtidal substrate.

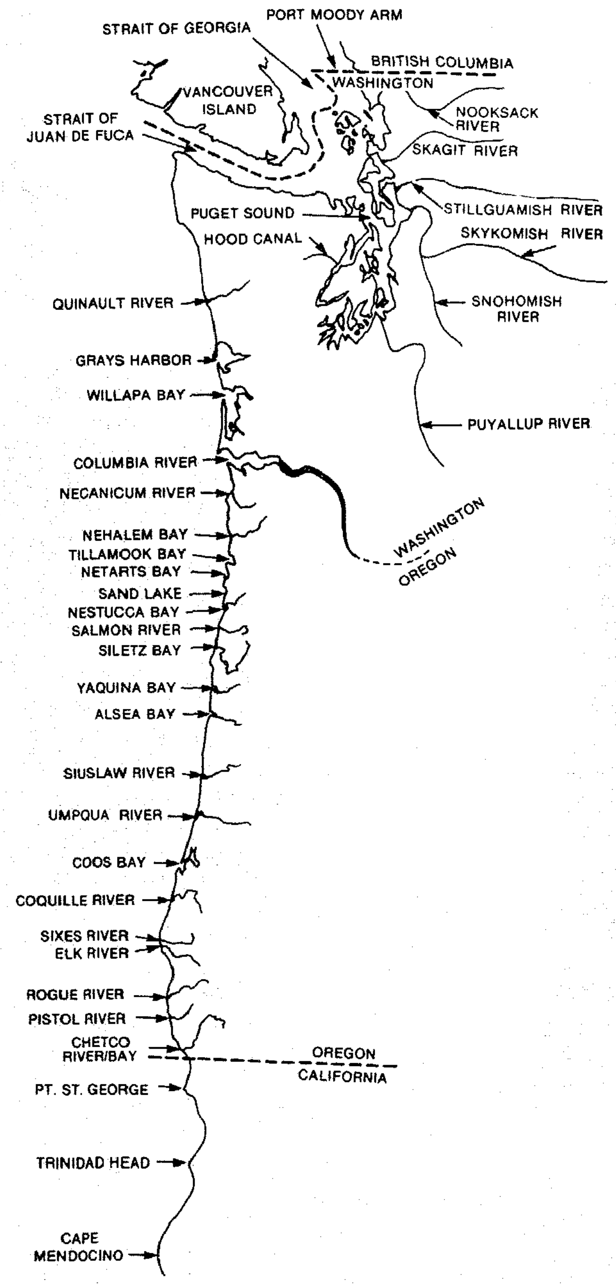


Fig. 1.1. Location of estuaries in Oregon and Washington.

1.3 METHODS

This community profile was constructed through a synthesis of the physiography, biota, ecological interactions, and effects of human manipulations in channel habitats of Pacific Northwest estuaries. Material was gathered from published as well as unpublished reports and other "gray" literature, some of which are cited as examples of the processes being described. Unless otherwise cited, interpretations and conclusions based upon unpublished data are solely those of the author.

Reference sources of particular use in this synthesis included the U.S. Fish and Wildilfe Service, Biological Services Program's Ecological Characterization of the Pacific Northwest Region (Proctor et al. 1980) and Pacific Coast Ecological Inventory (Beccasio et al. 1981).

CHAPTER 2

PHYSICAL DESCRIPTION OF ESTUARINE CHANNELS

2.1 DEFINITION AND DESCRIPTION

Although a diverse array of morphologies characterize Pacific Northwest estuaries, all basically meet the generally-accepted definition of Pritchard (1967), "An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with freshwater derived from land drainage." By this definition we exclude coastal lagoons, brackish seas, and saline lakes which have neither the dynamic tidal exchange of sea water nor riverine input of freshwater characterized by true estuaries and where riverine input is typically exceeded by evaporation. In the Pacific Northwest, however, estuarine "systems" such as Puget Sound and the Strait of Georgia also meet this definition of an estuary, but which, because of their predominantly marine nature, we will also exclude in favor of addressing the smaller estuaries found within them.

Within an estuary, channels are defined as, "an open conduit either naturally or artificially created which periodically or continuously contains moving water, or which forms a connecting link between two bodies of standing water" (Langbein and Iseri 1960). As such, channels constitute critical interfaces within the estuary itself, linking littoral and sublittoral, riverine and marine habitats. The relationship between estuarine channels and other components of the estuary are illustrated in Figure 2.1. Within this definition fall three basic classes of channels: mainstem channels (thalwegs of Proctor et al. 1980) wherein occurs the principal transport of water into and out of the estuary; subsidiary (stream) channels through which minor water transport occurs; and blind or tidal channels which primarily drain flats of tidally or flood-introduced water rather than runoff from associated wetlands and uplands. Examples of several of these classes of channels are found in the Fraser River estuary (Fig. 2.2).

2.2 GEOMORPHOLOGY

Pritchard (1967) and Russell (1967) also classified four types of estuaries based upon their geological origin and development: 1) drowned river valleys, which were produced by rises in sea level or subsidence of land; 2) fjords, wherein deep, U-shaped estuaries were formed by glacial action; 3) bar-built estuaries, created by accumulation of sediments across an open rivermouth or coastal bight; and 4) estuaries resulting from tectonic processes such as faulting. There is also at least one case in the Pacific Northwest of a fifth type of estuary, that created by man-made manipulations of river course and shoreline morphology.

Configurations of tidally influenced deltas which form intersections between estuarine channels and the ocean are governed by sediment dispersal and accumulation patterns. Wright and Coleman (1973), Coleman and Wright (1975), and Wright (1977) have suggested that these patterns are determined by the interaction between outflow dispersion (including

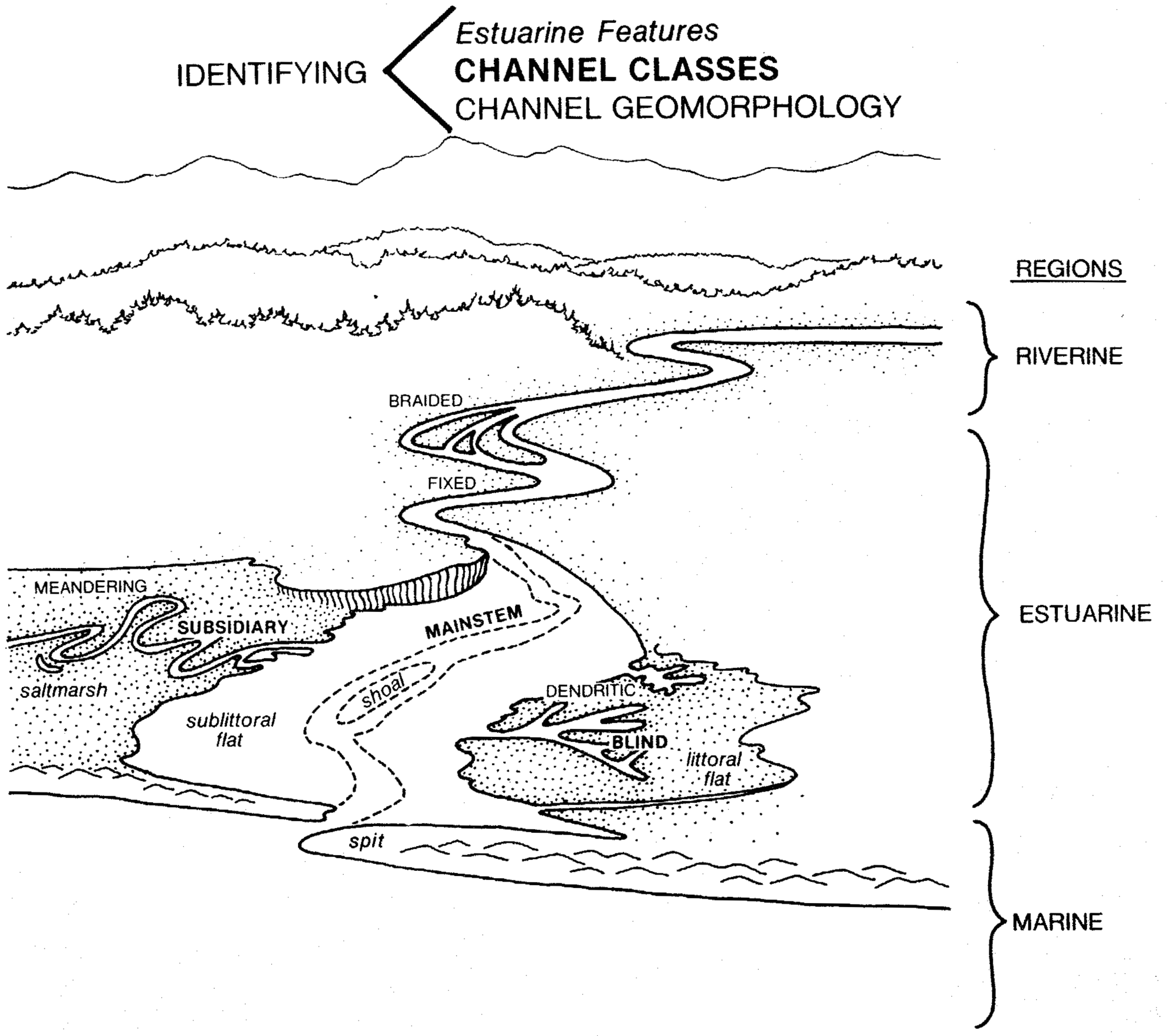


Fig. 2.1. Representative estuarine channel classes and geomorphologies and associated estuarine features and regions.

inertial, buoyancy, and frictional processes) and basinal processes (including waves, tides, longshore drift, ocean currents). In the absence of overpowering tide and wave effects, depositional patterns depend upon the relative dominance of: 1) outflow inertia, 2) boundary sheer stress seaward of the mouth, and 3) outflow stratification (buoyancy). Inertia-dominated effluents produce narrow river-mouth bars. Wright (1977) maintains that inertial effects are typically exceeded by either turbulent bed friction (boundary sheer stress) or effluent buoyancy (stratification), which results in triangular "middle-ground" bars with frequent channel bifurcation in the former case and narrow distributary mouth bars with elongate distributaries having parallel banks and few bifurcations in the latter case. Where tidal currents are typically stronger than river outflow (i.e., macrotidal

Fig. 2.2. Example of estuarine channel habitats in the Pacific Northwest; A) braided mainstem channels of main arm of Fraser River are separated by saltmarsh habitat, and B) a closer view of blind channels in saltmarsh habitat on Woodward Island (Photographs courtesy of David Levy, Westwater Research Centre, University of British Columbia, Canada).

environments), bidirectional currents create sand-filled, funnel-shaped distributaries in which linear tidal ridges have replaced the distributary mouth bar (Fig. 2.3A); where strong wave action intercepts the river mouth, constricted or deflected channels develop (Fig. 2.3B). Swift (1976) also developed categories of "tidal inlet" morphologies, including (1) overlap, (2) offset, and (3) symmetrical, which could be applied to Pacific Northwest estuaries. See Elliott (1978a and b) and Reineck and Singh (1980) for further discussion of delta and inlet structure.

The structure of estuarine channels reflects, in part, the origins and development of the estuary as governed by the dynamic forces of riverine and tidal components. Morphologies of channels usually reflect the original riverbed shape and pattern in drowned river valleys while channels in bar-built estuaries are often ephemeral in location and form. Given the glacial formation of fjords, channels in these estuaries tend to be stable and relatively permanent. This variation in stability is reflected in four basic channel configurations: 1) fixed channels, which were erosionally created, usually remain in the same location and the bed is deepened over time; 2) braided channels, which are characterized by many divisions into smaller branches around lenticular bars or islands, with the branches uniting at various downstream locations; 3) meandering channels, which have a simple, winding course that changes systematically over time; and 4) dendritic channels, which have irregular branches leading to a common channel.

The principal characteristics of the channel bank are its slope and substrate, which are not only correlated but are also affected by the orientation and velocities of the river and tidal currents at that point. Bank slope can be classified into four gradient classes: 1) vertical, 90°-45°; 2) steep, 45°-30°; 3) moderate, 30°-5°; and 4) shallow, 5°-0°.

Substrate can be defined as either consolidated (combined or firm rock or soil) or unconsolidated (loose and disassociated particles). Unconsolidated sediments can be classified on the basis of particle diameter as: 1) silt or clay, 2) sand, 3) gravel, 4) cobble, and 5) boulder and may be further divided within these categories (Appendix B). Further discussion of the sediment characteristics of estuarine channels is presented in Section 2.5.

One of the few detailed studies of estuarine channel morphology was Levy and Northcote's (1981) documentation of tidal (blind) channel characteristics in the Fraser River Estuary. Twenty-two habitat characteristics were measured at 18 separate blind channels, most of which were dendritic in character. The channels were further classified into four orders: 1) channels of large subtidal sloughs or reaches which never dewater at low tide; 2) large channels which experience high velocity tidal flows and usually do not dewater at low tide; 3) intertidal channels which branch off second order channels or sloughs and usually dewater completely at low tide; and 4) small intertidal channels which branch off second or third order channels and always dewater at low tide. These and several other characteristics may be utilized to define most blind and subsidary estuarine channels and some may be applied to the characteristics of mainstem channels (Fig. 2.4). Appendix C lists the measurements and the values which Levy and Northcote (1981) obtained from their characterization of tidal channel habitats in the Fraser River Estuary; the major descriptors of channel morphology indicated predominantly third order channels with relatively uniform total depths (D_C; $\bar{x} = 1.75 \pm 0.33$ m), trough depths (D_t; 8.69 ± 5.63 cm), and mouth widths ($W_1 + W_2$; 13.2 ± 6.0 m) but more variable total lengths (L_C; 579.6 ± 505.3 m), total area (A_t; $5{,}370.8 \pm 5{,}148.1$ m^2), and refugia area (357.9 ± 648.4 m^2). Their analyses of the relationship between channel characteristics and fish assemblage composition illustrated some significant associations between particular assemblages and channel characteristics, including channel morphology (see Section 6.2.2).

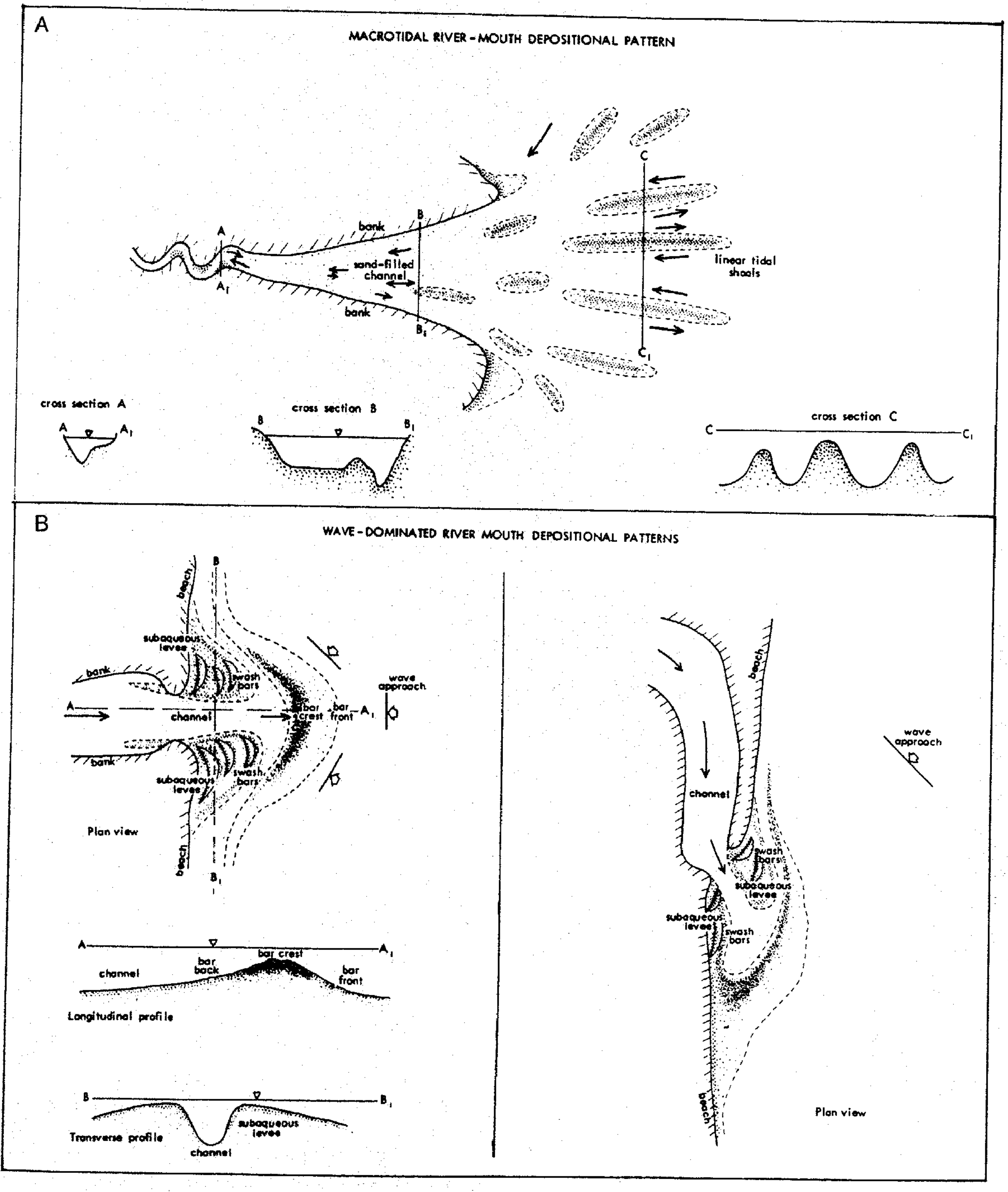
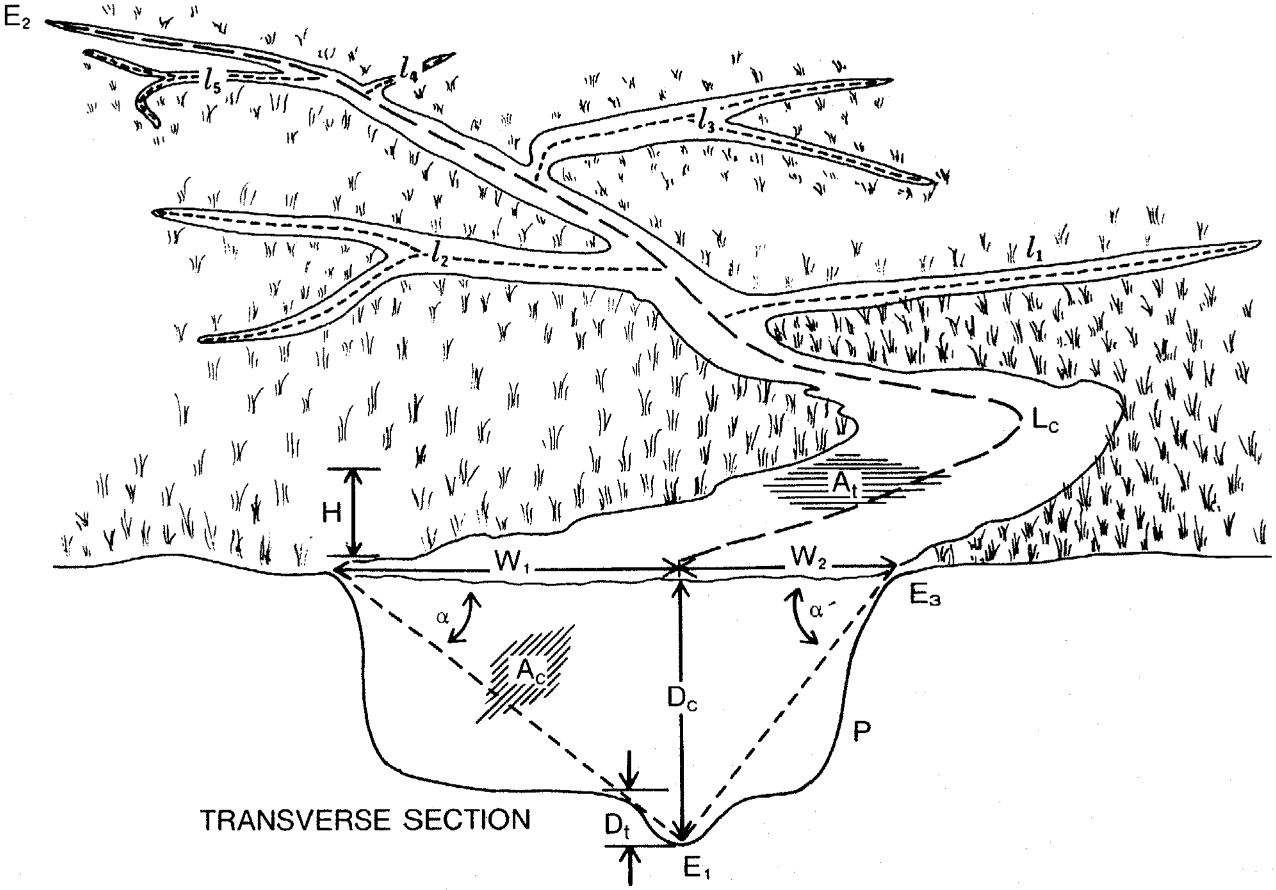


Fig. 2.3. Estuarine channel mouth depositional patterns associated with macrotidal systems in the absence (A) and presence (B) of strong wave action (from Wright 1977).



Measurements:

A_c = transverse area (m^2)

A_t = total area, typically measured by planimetry from charts (m^2)

D_c = total depth (m)

D_t = depth of trough in bottom of channel which usually carries residual tidal flow (cm)

E_1 = elevation of channel bottom at mouth (m)

E_2 = elevation of end of blind channel (m)

E_3 = elevation of surrounding bank (m)

H = height of surrounding vegetation; varies seasonally but typically measured at peak production period; (m)

L_c = axis length from mouth to furthest point on principal axis of channel (m)

l_{1-5} = length of subchannels (m)

W_1+W_2 = width between tops of banks perpendicular to axis of channel (m)

α and α´= bank angles as measured by $\tan^{-1} D_c/W_1$ and $\tan^{-1} D_c/W_2$, respectively; (°)

Channel Characteristics:

total length = length of main axis channel (L_c) and subchannels (l_{1-5}); (m)

perimeter = wetted perimeter (P) of main axis channel and subchannels; (m)

gradient = drop in elevation (E_2-E_1) between mouth and end of channel, divided by axis length (L_c); (m/m)

orientation = orientation of main axis from true north; (°)

average bank angle = mean of α and α´; (°)

angular deflection = angular deflection to prevailing flowing tide or river current; (°)

refugia area = area of watered pools remaining in channel at low tide; (m^2)

Fig. 2.4. Estuarine channel dimensional characteristics (adapted from Levy and Northcote 1981).

2.3 CIRCULATION

Estuarine circulation is usually described in terms of the role played by tidal currents relative to that of river flow and involves characterization of water movements, mixing processes, and the distribution of salinity and temperature resulting from these dynamic physical processes. The nature of tidal cycles can also influence estuarine circulation. In the Pacific Northwest, tides are purely diurnal or semidirunal for only a few days per month and are generally classified as mixed (Thomson 1981). A traditional scheme of classification (Stommel and Farmer 1952; Cameron and Pritchard 1963; Review by Bowden 1967) involves variations about the simplest relationship between river water and salt water, i.e., in the absence of other influences, the lower density river water will flow as a distinct layer, separated by a discernible interface, over salt water. The principal factors influencing this relationship include fresh water flow, tidal currents and resulting turbulence, the physical dimensions of the estuary, the Coriolis effect. As a result, four types of estuaries have been described around these variations: 1) salt wedge, which is river-flow dominated; 2) two-layer flow with entrainment, which is river-flow dominated as modified by tidal currents; 3) two-layer flow with vertical mixing, which is a combined effect of river flow and tidal mixing; and 4) vertically homogeneous, where tidal currents are the dominant physical process affecting circulation and where the degree of mixing may vary laterally. A number of cases exceptional to this classification scheme are also recognized as a result of mixing patterns in extremely complex estuaries (Bowden 1967).

In coastal plain estuaries (i.e., drowned river valleys and bar-built estuaries versus fjords), especially where they have been modified for navigation, the ratio of freshwater flow to tidal prism can be a general index of the mixing type (Schultz and Simmons 1957). A ratio >1.0 indicates a highly stratified type of estuary; around 0.25 indicates a partially mixed estuary; and >0.1 indicates a well-mixed estuary.

A further classification of estuaries proposed by Hansen (1965) and Hansen and Rattray (1966) incorporates two dimensionless parameters to describe the development of stratification and gravitational convection in estuaries. This approach utilizes stratification-circulation diagrams (Fig. 2.5) to describe a continuum of estuarine conditions where the ordinate of the figure is the ratio of the tidal-averaged salinity difference between the bottom and surface, $\delta S = S_b - \bar{S}_s$, to the depth- and tidal-averaged salinity (S_0) at a given location, and the abscissa represents the ratio of the tidal-averaged net circulation velocity at the surface, U_s, to the averaged, cross-sectional net river runoff flow velocity, U_f. This classification scheme distinguishes seven types of estuaries:

Well-mixed estuaries;

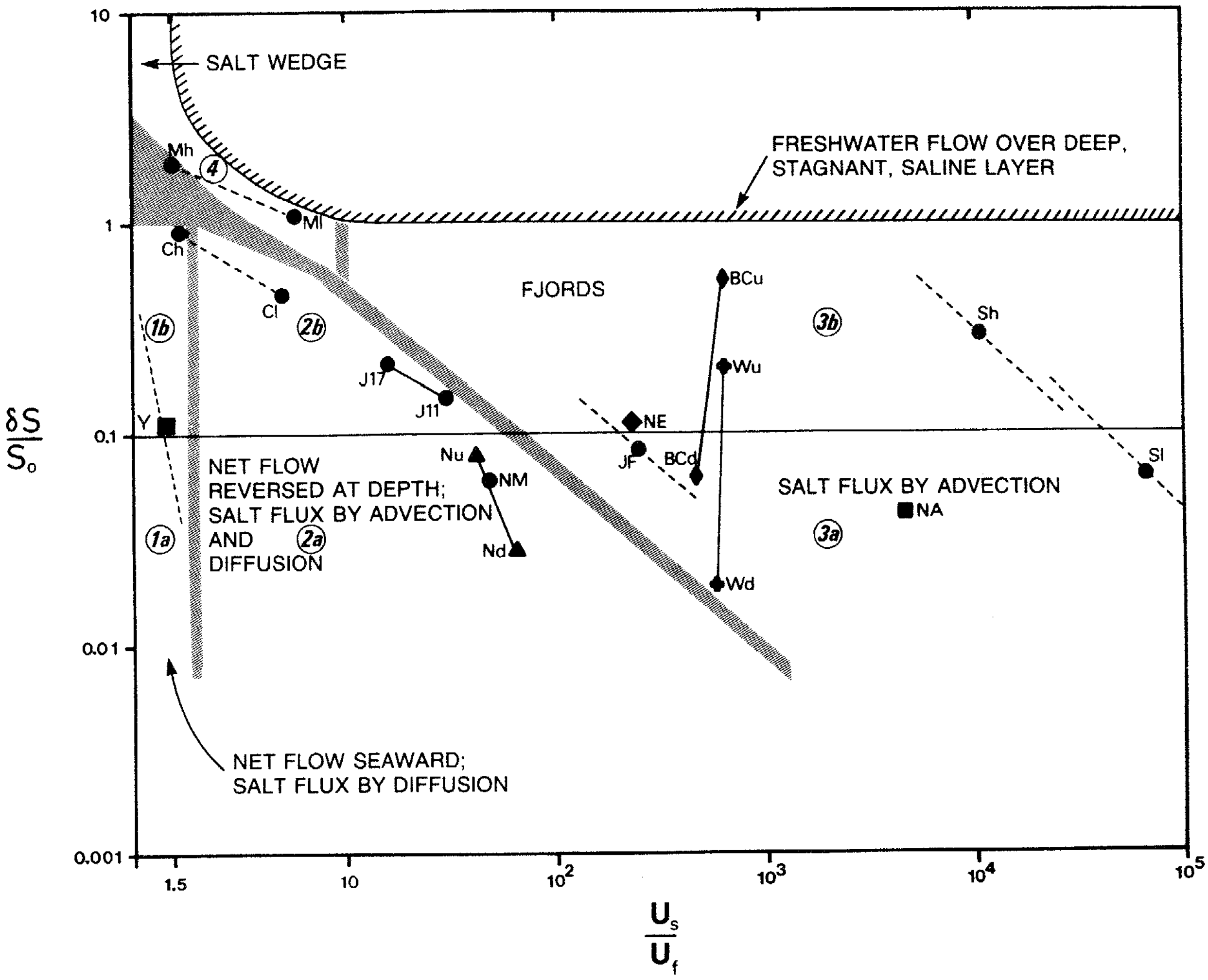
(1) type 1a, where the net flow is seaward at all depths and upstream transfer of seawater is controlled by diffusion and salinity stratification is slight, and
(2) type 1b, the variation of type 1 where there is appreciable stratification;

Partially-mixed estuaries;

(3) type 2a, where net flow reverses at depth and both advection and diffusion are important determinants of the flux of salt water upstream and stratification is slight, and
(4) type 2b, the variant to type 2 where stratification is prominent;

Fjord estuaries;

(5) type 3a, where advection dominates by accounting for over 99% of the upstream seawater transfer with little stratification, and
(6) type 3b, where the lower layer is so deep that the salinity gradient and associated circulation are effectively surface phenomenon; and,



LEGEND

M = Mississippi River
C = Columbia River estuary
J = James River estuary (numbers indicate miles from river mouth)
NM = narrows of Mersey estuary
JF = Strait of Juan de Fuca
S = Silver Bay

h = high discharge periods
l = low discharge periods

Y = Yaquina Bay at mile 14
N = North River
BC = Bay Center
W = Willapa River

u = upstream
d = downstream

NA = Nahcotta Channel
NE = Nemah River

Fig. 2.5. Estuarine classification diagram illustrating seven types of estuarine circulation (circled numbers, letters) from Hansen and Rattray (1966). Data point for Yaquina Bay is from Callaway (1971) and data for Willapa Harbor is from CH$_2$M-Hill (1981).

Salt-wedge estuary;

(7) where the archetypical stratification is well developed.

But as a result of extremes in stratification in the upper vs. lower reaches of an estuary and in river discharge, the estuaries can actually span several classifications, as indicated by the lines connecting or extending the various sample points in Fig. 2.5. Using this scheme, Hansen and Rattray (1966) compared the Columbia River estuary (drowned river valley) with the Strait of Juan de Fuca (fjord). They illustrated that the Columbia River estuary actually shifted from a type 1b to a type 2b in response to decreasing river flow while the Strait of Juan de Fuca fell into a type 3a estuary. They also included four other estuaries for comparison (Fig. 2.5). CH_2M-Hill (1981) also indicated that five sites in Willapa Harbor (also included in Fig. 2.5) sampled during June fell within or between type 3a and 3b. Classifications of some of the larger estuaries have been assigned in Section 2.6.

The configuration of the mouth of the estuary can have a marked effect on the dynamics of tidal circulation through the estuary. Goodwin et al.'s (1970) tidal analysis of three Oregon coastal estuaries indicated that the more constricted entrances to Alsea and Siletz Bays produced "choking" of tidal amplitude and truncation of tidal amplification at the entrance to the estuary which was not evident in Yaquina Bay. Tidal currents also tended to reach higher maxima in the constricted, "choked" estuaries (over 2 m sec^{-1} in Siletz Bay, 1 m sec^{-1} in Alsea Bay, and 0.6 m sec^{-1} in Yaquina Bay). Phase shifts between tidal elevations and tidal currents of 90° to 100° and the temporal distribution of tidal amplification through the three estuaries also indicated the presence of (progressive) reflected or resonating waves.

One dimensional, vertically-integrated models of circulation in the Fraser River estuary (Crookshank 1971; Ages 1979) have been utilized to document the interactive effect of tides and river discharge upon water surface elevations. They illustrate that river discharge contributes progressively more to the rise and fall of water surface elevation at points further up (upriver) the estuary and that, as discharge increases, the point where the daily tidal fluctuations (rise and fall of water) cease to exist moves down the estuary. One of the more interesting simulated characteristics of that estuary was a significant time lag between the upriver propagation of the flood and ebb tides (e.g., ebb tide taking two hours to move the same distance that the flood moved in one hour).

Few studies have compared or classified circulation among different classes of estuarine channels or within channel systems. Officer (1976) provides the most detailed and quantitative information to date. While many of the above schemes can be applied broadly to estuarine channels, there are a number of factors, such as winds, basin (bottom) and channel bathymetry, and coastal storm surges, each of which may become more important in affecting circulation patterns on the small scale. For example, Pethick (1980) indicated that shallow water asymmetric tides are responsible for velocity asymmetry and dendritic channel morphology is responsible for the position and strength of velocity surges within tidal channels.

2.4 WATER MASS CHARACTERISTICS

2.4.1 Physical

Physical characteristics of the water masses occupying estuarine channels exhibit broad spatial and temporal variation due to the flux and mixing of different water masses over short-term (i.e., tidal), intermediate (i.e., storm event), and long-term (i.e., seasonal cycles). While some features of any one water mass may be relatively predictable, e.g., tidal volume, the synergistic interactions among riverine, marine, and ambient estuarine water masses and meteorological events create basically stochastic (random) patterns of water volume, velocity, temperature, sediment content (turbidity), and density over time. The variation of these parameters also changes with physical location in the estuary in response to the proportional representation of the three basic water masses and basin configuration.

Total water volume of an estuary generally depends upon riverine runoff and tidal influx. Runoff volume depends upon precipitation regimes and the drainage basin of the rivers and tributaries to the estuary. Given the range in size of drainage basins contributing to Pacific Northwest estuaries, from 6.68 x 10^5 km^2 for the Columbia River to less than 20 km^2 for many small estuaries along the coast, the range in average annual discharge volume is correspondingly high; from over 7,600 m^3 sec^{-1} for the Columbia River to less than 20 m^3 sec^{-1} for small streams, respectively. Short-term fluctuations, however, may be very dramatic, especially during winter storm events. For example, short duration winter storm freshets in the Columbia River can actually exceed the annual sustained summer freshet of over 14,000 m^3 sec^{-1} (Fox 1981). Flushing times, in terms of the number of tidal cycles required to replace the estuary's volume, vary as a function of river discharge and coastal upwelling (Duxbury 1979). Summer flushing times for seven coastal estuaries, summarized by Johnson and Gonor (1982), vary between 4 to 5 tidal cycles (Salmon and Netarts Rivers estuaries) compared to 60-68 tidal cycles (Coos Bay). Neal (1965) estimated flushing times for the Columbia River estuary to be between two and ten tidal cycles. Pearson and Gotaas (1951), Callaway (1965), and Stein and Denison (1965) estimated average flushing times for Grays Harbor of between 5 and 48 days (10 and 96 tidal cycles) depending upon river flow values. Using a water mass budget approach, Duxbury (1979) estimated monthly replacement rates of between 20% (June) and 166% (January) day^{-1} and corresponding residence times of 5.0 and 0.60 days, respectively, for inner (upper) Grays Harbor estuary. Flushing times of coastal estuaries in the Pacific Northwest, however, may be highly variable depending upon nearshore ocean conditions. In Willapa Bay a strong northwesterly wind during the summer can bring upwelled water into the bay from the ocean, promoting rapid flushing. At other times the Columbia River plume may essentially block the turnover of bay and ocean water masses, and complete flushing at such times could take more than 20 days (U.S. Army Corps of Engineers 1976). Flushing times of within-channel water masses have not been addressed, but, given the fact that most of the transport occurs through these channels, we might safely assume that they are somewhat shorter than those of the estuary as a whole.

Temperature regimes in estuarine channels reflect the influence of both exogenous riverine and marine water masses as well as endogenous estuarine water masses transported off sublittoral and littoral flats. Mixing of these three water masses within the channel habitat creates a temperature structure which varies in a conservative manner according to the relative contribution of each water mass. Marine waters represent the least variable temperature source. There is only a narrow seasonal range between 3°C and approximately 17.0°C depending upon the presence and extent of coastal upwelling (McGary 1971; Oregon State University 1971; Proctor et al. 1980) and the influence of riverine plumes from major sources such as the Columbia (McGary 1971), Fraser (Waldichuck 1957; Tabata 1972), and Skagit Rivers (Cannon 1978). River temperatures tend to exhibit a greater temperature range over time, ranging from 0°C to over 25°C depending upon air temperature, precipitation, solar incidence and snow/glacial runoff. The waters in an estuary's channels are derived ultimately from exogenous sources which are entrained over littoral and upper sublittoral flat habitats during flood tide cycles and riverine flood events. Heating or cooling of the flats prior to and during the period of inundation can result in rapid and extreme elevation or depression of ambient water mass temperatures.

The result of the dynamic mixing of these water masses within the channels reduces the temperature extremes but still allows considerable short-term (within tidal cycles) variation. Temperatures in channel habitats in the Columbia River estuary range between 5°C and 25°C (Park et al. 1972); 5°C and 20°C in Grays Harbor (Loehr and Collias 1981); and 4°C and 23°C in the Duwamish River estuary (Lenarz 1969). Tidal effects caused temperatures in the Salmon River estuary to fluctuate from 7.3°C due to the presence of marine water on incoming spring tides to 18.2°C on outgoing tides when river water was present (Johnson and Gonor 1982). Fine-resolution sampling of temperature and salinity at one station in the Salmon River estuary through a complete tidal cycle (Johnson and Gonor 1982) illustrated that the temperature of the water mass measured late in the ebb tide originated in a low salinity water mass from at least 3 km up the estuary.

Sediment is transported into or through the estuary in suspension or in boundary layer flow along the bottom as bed load. Accordingly, sediment load and the sources of the sediment within the estuarine channel vary seasonally with river discharge and tidal flux (Boggs and Jones 1976; Scheidegger and Phipps 1976).

Suspended sediment is composed principally of sand and finer particles and varies with water depth and velocity. Suspended sediments in the Columbia River above the estuary consist of particles <63 m in diameter and the total suspended load into the estuary, which can vary threefold from year to year, was estimated to be 9.5×10^{6} tons yr^{-1} (Haushild et al. 1966). Suspended sediment concentrations can vary from 12.0 to 38.5 mg L^{-1} at the surface, 12.5 to 69.6 mg L^{-1} within the salt wedge and 12.5 to 59.9 mg L^{-1} 1 m above the bottom, depending upon location in the estuary, tidal stage, and current velocity (University of Washington Department of Oceanography 1980). Total mean sediment flux in drainage channels in the lower estuary in February 1980 ranged between 0.2 and 1.0 mg cm^{-2} sec^{-1} at Chinook and Sand Island and between 0.1 and 0.7 mg cm^{-2} sec^{-1} at Ilwaco.

2.4.2 Chemical

Estuarine mixing of the highly variable concentrations of dissolved salts and compositions of dissolved material characteristic of river waters with the relatively uniform chemical composition of coastal sea water produces a characteristic mixing series between dilute and saline end-members (Burton and Liss 1976). Composition of river waters is influenced by precipitation and rock and soil weathering. As a result, considerable variation occurs as a result of the geological character of the drainage area and differences in the proportional contribution of ground water flow and surface runoff (Livingstone 1963; Gibbs 1970). In general, calcium, bicarbonate, and silicate are usually the major dissolved constituents in river waters, while sodium, magnesium, chloride and sulfate predominate in sea water. In that sea water salts comprise approximately 28% of the dissolved material at $5\,^{\circ}/_{\circ\circ}$ salinity, the chemical composition of seawater predominates early in estuarine mixing processes (Burton and Liss 1976).

This relationship was best illustrated for the Columbia River estuary (Park et al. 1972), where SiO_2 (250-0 μM), O_2 (6.5-0.5 ml L^{-1}) and winter NO_3 (35-0 μM) could be attributed to river sources while PO_4 (2.0-0 μM), total CO_2 (2.0-1.0 μM), alkalinity (2.0-1.0 meq L^{-1}), and summer NO_3 values (20-0 μM) originated principally from oceanic water masses. A recent review of historical water quality data in the Columbia River estuary (Pacific Northwest River Basins Commission 1980) indicated considerable seasonal variation in nutrient concentrations although nutrient patterns had changed little over the last 20 years. Representative summer nutrient values were 0.002 mg L^{-1} PO_4-P, undetectable nitrate, and 4.0 mg L^{-1} SiO_2 in riverine portions of the estuary and 0.070 mg L^{-1} PO_4-P, 0.20 mg L^{-1} NO_3-N and 2.0 mg L^{-1} SiO_2 in marine regions; the data suggested nitrate and phosphate depletion occurs within the estuary during late summer although coastal upwelling may increase nutrient levels (NO_3, PO_4) in the lower estuary during the summer (Haertel et al. 1969; Oregon State Univ. School of Oceanography 1980b). In comparison, spring and summer values of NO_3-N and total PO_4-P in the Grays Harbor estuary ranged between 0.018 and 0.055 mg L^{-1} and 0.003 and 0.060 mg L^{-1}, respectively (Herman 1975).

Although it is probable that nutrient inputs into estuarine channel habitats are artificially elevated during periods of high river discharge due to runoff of nitrogen and phosphorus from agriculture and silviculture-applied fertilizers in the watershed, no causal data is available for Pacific Northwest estuaries. Collias and Lincoln (1977), however, calculated that the average inflow of phosphate into the main basin of Puget Sound was 1,223 metric tons and the contribution of phosphate from all sewers was 12.6 metric tons, compared to 18,400 metric tons of phosphate in the main basin at any given time.

Salinity has traditionally been employed as an index of mixing, although this has been criticized because the definition of salinity depends upon the essential constancy of the relative proportions of the dissolved ions in sea water and the introduction of river water causes departures from the nearly constant ionic ratios of oceanic waters (Burton and Liss 1976). As indices of mixing, chlorinity, chlorosity or isotopic oxygen ratio ($^{18}O/^{16}O$) values have also been suggested as suitable parameters (Boyle et al. 1974), but of these only chlorinity has been measured frequently in estuarine channels of the Pacific Northwest. Considering that our primary concern in this synthesis is the biological structure and dynamics of estuarine channel communities, the spatial and temporal distribution of salinity structure in the estuary is an appropriate indication of the major chemical factors structuring these communities (Caspers 1967).

Saline oceanic water is transported into an estuary by both advection and diffusion (Bowden 1967). Advected oceanic water masses are generally referred to as the "salt wedge" although diffusion processes can cause the intrusion of saline water beyond the upstream limit of the salt wedge. In such estuaries as the Columbia River, it appears that longitudinal salt transport via diffusion may be significant (Hansen 1965; Hughes 1968; Dyer 1973; Hughes and Rattray 1980; Fox 1981). Salinity gradients can be distinct and sharp in situations where fresh and saline water masses are stratified, or broad and variable where vertical mixing predominates. Thus, the degree of both salinity intrusion and stratification is dependent upon estuary morphology, river discharge, semi-diurnal and spring-neap tidal cycles, and short-term, stochastic events such as storms; in terms of estuary morphology, the rate of change of cross-sectional area through the estuary and the bed topography are important factors determining salinity distribution (Prandle 1981).

Although most simulation models of estuarine circulation, such as those produced for the Fraser River estuary (Crookshank 1971; Ages and Woollard 1976), are vertically integrated (or, at best, integrate over two depth sectors), accurate descriptions of current flow must take into account the dynamic effect of salinity intrusion upon currents. Detailed empirical studies are required before more complex models can be assembled. Such field documentation in the Fraser (Ages 1975) has illustrated the role of the salt wedge in modifying the tidal effect upon surface outflow. In this instance, the salt wedge continues its upstream motion after flood slack, then retreats down the estuary but maintains its shape until it is finally carried out as a homogeneous water mass. In the Columbia River estuary, saline water can be detected as far as 42 km upriver under the combination of extremely low river discharge and neap flood tides, but only as far as 10 km under high river discharge, with stratification more pronounced during neap tidal cycles than spring tidal cycle (Hansen 1965; Dyer 1973; McConnell et al. 1979; Jay 1981; Fox 1981). It should be noted, however, that the archetypical salt wedge is not generally found in the Columbia River estuary

(D. Jay, Univ. Wash., pers. comm.).

Loehr and Collias (1981) indicated that the extent of salinity intrusion in Grays Harbor in June and July 1966 (river flows, 49.1 m^3s^{-1} and 68.4 m^3s^{-1}, respectively) varied according to the range of tidal cycle (i.e., neap vs. spring). The extent of intrusion shifted four miles over the tidal cycle during a neap and less than a mile during a spring tidal cycle. Simenstad and Eggers (1981) indicated that salinities in channel habitats between March and October 1980 were relatively uniform (well mixed) in the central portion of the estuary (Cow Point, Moon Island), but typically stratified at the upper (Cosmopolis) and lower (Stearn's Bluff) extremes of mixing zone. Salinities at the latter two sites ranged widely between 5°/oo and 28°/oo but covered a narrower range between 25°/oo and 36°/oo at the site (Westport) near the mouth of the estuary.

Salinity ranges at three channel sites (RM 1.0, 2.2 and 3.7) in Yaquina Bay betwwen 1960 and 1973 were 11.7°/oo (34.1-22.4°/oo; $S\bar{x}$ = 29.7°/oo) at the lower end of the estuary, and 16.3°/oo (34.1-17.8°/oo; $S\bar{x}$ = 28.2°/oo) and 24.1°/oo (33.5-9.4°/oo; $S\bar{x}$ = 27.3°/oo) further up the estuary (U.S. Army Corps of Engineers 1975).

Levy and Levings (1978) documentation of surface salinity at a channel in the Squamish River estuary also indicated the broad seasonal fluctuations which can exist at one site. The maxima of 26-27°/oo occurred in the winter and less than 4°/oo sustained during the spring and summer months. This seasonal effect was also illustrated for a blind, dendritic channel habitat in the Fraser River estuary (Kistritz and Yesaki 1979), where water flooding the channel and marsh was brackish (3-8°/oo) only during high winter tides, despite the greater tidal range during the summer ($\sim$5 m) than the winter ($\sim$3 m).

River waters are typically more acidic than sea water but pH gradients in estuarine channels are also affected significantly by variations in the chemical composition of the mixing water masses. pH values in the Columbia River estuary range from 5.8 to 8.3 but usually fall between 7.6 and 7.9 within the mixing zone; tributary channel waters in the area of Youngs Bay have been reported to be slightly more acidic than main channel water in the adjacent estuary (Park et al. 1980; Pacific Northwest River Basins Commission 1980). Herrman (1975) documented spring-summer pH values between 6.94 and 7.25 in the upper Grays Harbor estuary, with the surface waters usually 0.08 pH units less than the more saline bottom waters. A 13-year water quality data base for Yaquina Bay (U.S. Army Corps of Engineers 1975), however, illustrated quite uniform pH values at three locations through the estuary (at river miles 1.0, 2.2 and 3.7), with ranges between 7.6 and 8.6 (pH $\bar{x}$ = 8.1 at all three locations).

Dissolved oxygen (DO), in addition to being the essential element in aerobic metabolism by aquatic organisms, is involved in the biochemical breakdown of organic matter in marine environments. In essence, aquatic organisms are constantly competing for free dissolved oxygen and will incur physiological limitations when dissolved oxygen levels decrease below approximately 5 ppm; the tolerance to depressed dissolved oxygen is highly variable among aquatic organisms, however, and many naturally divergent structures of marine water column and benthic communities are due to different dissolved oxygen regimes.

Due to mixing of riverine and marine water masses and their typical rapid flux through the habitat, estuarine channels typically do not experience dissolved oxygen depletion except during situations of seasonal minima in water exchange or due to increased organic loadings by organic pollutants.

Dissolved oxygen is considered to be principally regulated by: 1) the rate of addition of biological oxygen demand (BOD); 2) the net rate of addition or removal of oxygen by benthic oxygen demand, photosynthesis, and respiration;

3) the rate of reaeration; and 4) the rate of removal of BOD by sedimentation or absorption (Dobbins 1964). Longitudinal dispersion, the rate at which a material is dispersed by eddies and diffusion, is not usually a significant factor in lacustrine and stream systems but is thought to be more important in estuarine channels. Gunnerson (1966, 1967) and Thomann (1967) provide evidence that patterns of dissolved oxygen concentration in estuaries may be highly periodic, potentially exhibiting annual, 14-day, 24-hour, and 12-hour cycles with the low frequency effects being relatively more important than those attributable to high-frequency phenomena. These cycles could be reasonably correlated to daily and spring-neap tide variations, solar radiation intensity, and photosynthesis.

Lenarz's (1969) detailed analysis of water quality data from the Duwamish River estuary indicated that the lowest concentration of dissolved oxygen in the channel probably was associated with the upstream edge of the salt wedge. Streamflow was positively correlated to dissolved oxygen concentration and this relationship was attributed to increased turbulence (diffusion), lower retention time, and greater dilution of BOD with increased streamflow. The timing of algal blooms, which often increased dissolved oxygen concentrations dramatically, were also determined to be related to streamflow and tidal prism.

Dissolved oxygen levels in estuarine channels of the Pacific Northwest are naturally high, being at or near saturation, except in a few highly developed estuaries with high BOD loadings. The Columbia River estuary represents the Pacific Northwest coast's largest system relative to natural dissolved oxygen concentration. Most estuarine waters are usually supersaturated (8-6 mg L^{-1}) during spring and summer months and slightly undersaturated (<6 mg L^{-1}) during fall and winter months; photosynthesis is considered to maintain the supersaturation state while biochemical oxidation and respiration reduces the saturation during fall and winter (Park et al. 1972). Oxygen depletion (<4 mg L^{-1}) often occurs in marine water masses during summer months when coastal upwelling causes low oxygen water masses to intrude into the estuary.

Wind and waves appear to be important factors determining dissolved oxygen levels in Willapa Bay, a large, relatively shallow natural coastal estuary. Maxima of up to 15 mg L^{-1}, occur in the winter, normal levels are 8 to 11 mg L^{-1}, and summer values range between 6 and 9 mg L^{-1}. Summer values are comparatively low because of higher temperatures and coastal upwelling of oxygen-depleted intermediate water (U.S. Army Corp Engineers 1976).

Grays Harbor, a coastal estuary with historically higher BOD loading than the Columbia River estuary, has exhibited dissolved oxygen depletion during low-flow summer months, when a tidal water mass with dissolved oxygen levels as low as 2 mg L^{-1} moved through the channels of the inner estuary with tidal action (Loehr and Collias 1981). Surface water dissolved oxygen at five channel sites in Grays Harbor between March and October 1980 were typically below saturation (65% min.) in the upper estuary and above saturation in the middle and lower regions of the estuary (Simenstad and Eggers 1981).

Similar dissolved oxygen depletion has been reported for Coos Bay, another highly industrialized estuary, where dissolved oxygen concentration of 1 to 2 mg L^{-1} occurred during late summer and early fall when the BOD of organic wastes was added to the water masses already depleted by the influx of oceanic water during low river discharge (Pacific Northwest River Basins Commission 1971). The lowest dissolved oxygen concentrations have been documented within the dredged channel of the Isthmus Slough, which is poorly flushed, is heavily industrialized, and includes log storage (Oregon State University 1977).

Lenarz's (1969) analysis of eleven months of high resolution monitoring of water quality in the channel of the Duwamish River estuary documented dissolved oxygen depression below 5 mg L^{-1} during several periods in the summer; the lowest values, 3 to 4 mg L^{-1}, were associated with the upstream edge (bottom) of the salt wedge.

Biochemical oxygen demand has not been as widely reported as dissolved oxygen. Five-day BOD levels in Yaquina Bay averaged 1.2 mg L^{-1} throughout the estuary and a maxima of 6.6 mg L^{-1} was recorded within two miles of the mouth (U.S. Army Corps of Engineers 1975). Summer values in Grays Harbor ranged between 1.45 to 5.13 mg L^{-1} (Herrman 1975).

2.5 SUBSTRATE CHARACTERISTICS

2.5.1 Physical

Channel substrates reflect both historic and extant conditions. The geological history of the estuary and its watershed determines the characteristics of the material through which the channel is being cut and of the sediment load borne by riverine currents. Dynamic hydrological, tidal, and meterological forces, however, affect the complex erosion and deposition processes which are constantly structuring the channel. The reader is referred to Elliott (1978a & b) and Reineck and Singh (1980) for more detailed discussions of sedimentation processes.

Erosion can occur through corrosion (chemical), corrasion (mechanical), and cavitation (Morisawa 1968), aided by the sucking, lifting forces of vortex action (Matthes 1947). Under vortex action loosened materials are sucked upward and downstream with the vortex current. Local discontinuities or separations of flow occur where there is a change in current direction and velocity caused by obstacles or impingement on channel walls. The result is a nonuniform distribution of energy at that point, which produces a veering and overturning of water masses as spiral flow. Water velocity, size of obstructions, spacing and size of obstacles and the sharpness of channel bends dictate the amount of separation, turbulence, and vortex action.

Besides growing deeper or cutting new beds, channels also widen by lateral corrasion and weathering of the walls during high water flow, which includes tidal influxes. Both channel cutting and widening are mediated by the resistance of the bed material. The critical erosion velocity of unconsolidated material varies as a function of the grain size. Hjulstrom (1935) indicated velocity decreased from $\sim$200-500 cm sec^{-1} ($\sim$4-10 knots) for particles 1 μm dia. to $\sim$20-50 cm sec^{-1} ($\sim$0.4-1.0 knots) for particles between 100 μm and 1 mm, and increased to 500 cm sec^{-1} ($\sim$10 knots) for particles as large as 100 mm dia. As a result, erosion of sand requires lower velocities than of either silt or gravel. Sternberg (1967) estimated that the critical drag velocity required to initiate general sediment motion in a Puget Sound channel was 2.2 cm sec^{-1} for sediment grain sizes between 0.3 to 1.1 mm dia.

Particles entrained and transported by a water mass are deposited when the current is no longer sufficient to carry them either as suspended particles (sediment load) or as bottom transported (bed load) particles. Deposition of the sediment load occurs with loss of competence caused by a decline in gradient, a reduction in velocity or a decrease in volume. Settling velocities range from 0.1 cm sec^{-1} (0.002 knot) for particles $\sim$20-30 μm dia. to $\sim$100-300 cm sec^{-1} ($\sim$1-6 knots) for particles 2-10 cm dia. (Hjulstrom 1935; Sundborg 1956). These relationships vary as a function of the characteristics of the particle (e.g., specific gravity) and water mass (e.g., salinity).

Thus, the dynamic changes in velocity, direction, sediment load and density of water masses moving through estuarine channels results in spatially and temporally variable sediment structure through the estuary, and with considerable variability among estuaries. A particularly prominent feature to most estuaries is a zone of minimum sediment particle size which typically occurs within the "mixing," "entrapment," "turbidity maximum," or "null" zone where upstream bottom tidal currents approximately balance downstream river currents (Arthur and Ball 1979; Cloern 1979). Maximum settling of suspended particles occurs within this zone during slack water, but much is resuspended during flood or ebb currents. The mixing of riverine and saline water masses also results in the flocculation of fine particles, both sediment (clay) and organic detritus, and these aggregates settle within this entrapment zone.

Hubbell and Glenn (1973) documented that the mean size of channel sediment in the Columbia River estuary became progressively finer downstream through the fluvial and transitional regions, only to become coarser in the marine region of the estuary. This relationship was verified in the more detailed CREDDP[2] studies of the Columbia River estuary. The sediment particles in the main channel were shown to decrease in modal size from 500-300 μm (1.00-1.75ϕ) off Grays Bay to 300-175 μm (1.75- 2.50ϕ) off Baker Bay (Roy et al. 1979; University of Washington Department of Oceanography 1980). Variation in channel sediment structure, however, is widely apparent and can be related to the current speed and the extent of communication with riverine or tidal flow (University of Washington Department of Oceanography 1980). Sediments in channels with open communication with the Columbia River, one of the estuary's major tributaries, or the density-driven flow from the ocean, tend to be coarser than sediments on adjacent sublittoral or littoral flats. Where water flow is restricted to only one end of the channel the sediment grain size is usually finer than on the adjacent flats. Channel bathymetry may also affect these relationships, as fine-grained sediments may also be found in deep segments of large channels where there are low velocity water areas below channel sill depths.

These relationships between sediment structure and channel morphology have also been illustrated within Coos Bay, where Hancock et al. (1980) illustrated that sediment grain size remained relatively constant (250 μm) within the Coos navigation channel but was an order of magnitude finer (62 μm) in Isthmus Slough, which does not have significant fresh water current flow through the channel.

Differential distribution of sediment composition is also well illustrated in Phipps and Schermer's (1980) data for the bottoms and slopes of the Grays Harbor navigation channel (Fig. 2.6). Gravel and coarse particles from riverine sources tended to be distributed in the highest and lowest reaches of the estuary, indicating both riverine and marine sources. Silts and clays accumulated within the mixing zone, probably more the result of flocculation processes than of settling. Fines (predominantly sand) composed most of sediments in the lower estuary and probably represented settling from both riverine and estuarine water masses. The principal difference between bottom and slope habitats was the longitudinal position of the peak occurrence of gravel, which was lower in the estuary in the channel bottom sediments. This probably reflected the higher current velocities along the bottom of the channel.

Sediments in the mainstem channel of Yaquina Bay fall into three realms of deposition (Kulm and Byrne 1967). The marine realm, extending 3 km into the estuary from its mouth, contains well-sorted, subangular to subrounded, fine to medium sand. The marine-fluviatile realm, occurring between 3 km and 10 km from the mouth of the estuary, has sediments with a wide range in texture, from well- to poorly-sorted, angular to subrounded silt to medium sand. The fluviatile realm in the upper reaches of the estuary further than 10 km from the mouth is characterized by sediments which are poorly sorted, angular to subangular grains of silt to coarse sand. Grain size in the lower 10 km of the estuary averages 217 μm (150-291 μm) and 279 μm in the channel above 10 km.

The only comprehensive study of subsidiary and blind estuarine channels in the region, that of the Westwater Research

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[2] Columbia River Estuary Data Development Program.

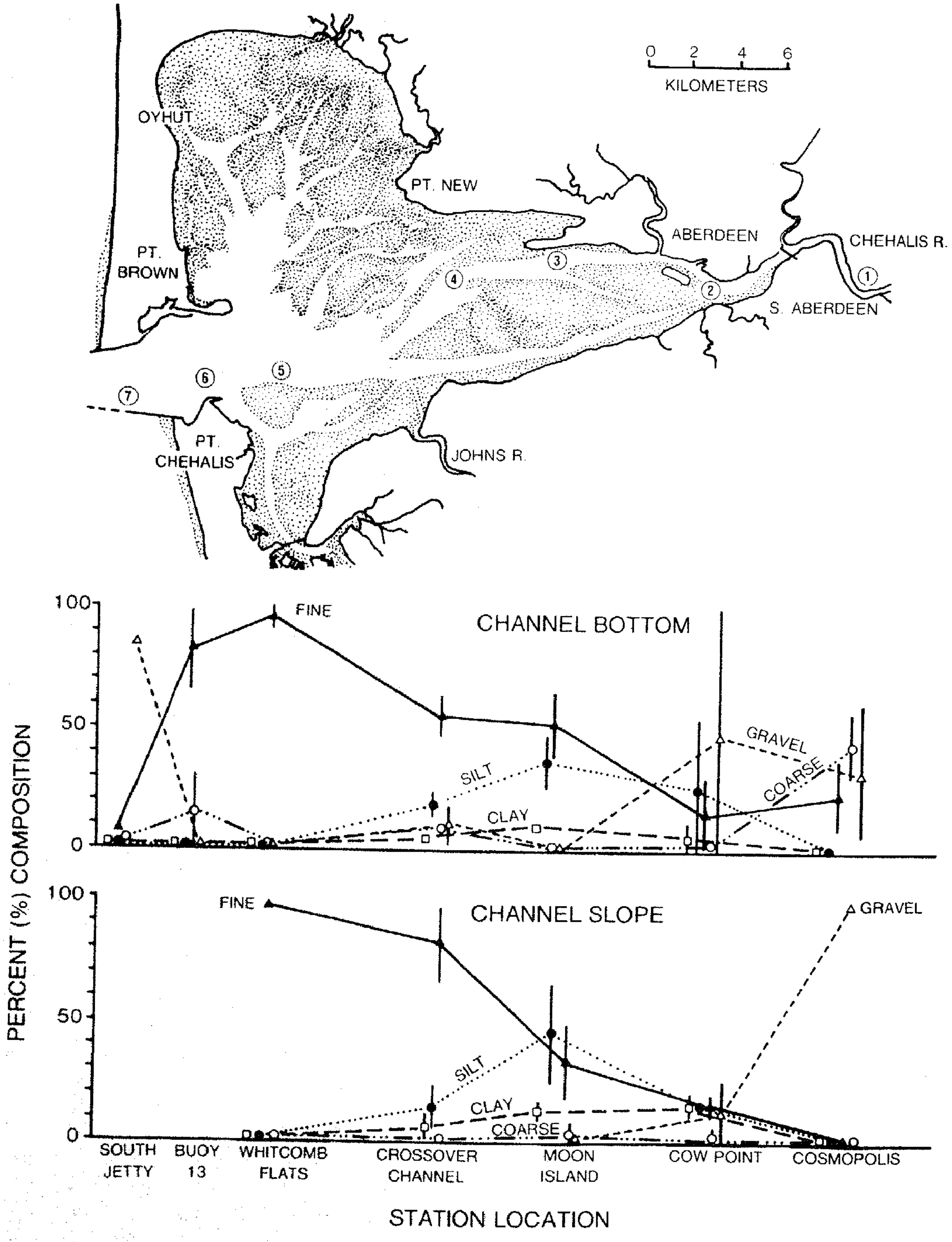

Fig. 2.6. Sediment size fraction (% wet weight) distributed at seven channel bottom and slope locations in Grays Harbor.

Centre, University of British Columbia studies in the Fraser River estuary, described sediments from the center troughs of dendritic channels at Woodward and Barber Islands and Ladner Marsh as being sandy, with the grain size ranging between 75 m and 192 m (Levy and Northcote 1981). Smith's (1980a) studies in northern Puget Sound indicated sediments from a dendritic channel along the delta of the North Fork Skagit River were composed predominantly of sand (81.13% by weight) and silt (15.32%), with mean grain size of 97.4 μm (3.36 φ). Sediments from the bank (+ 1.0 m elevation MLLW) of a principal tidal channel away from the delta were coarser (229.2 μm [2.13 Φ]) and sandier (89.88%), and had a greater sand to mud ratio (8.88) than did the sample from the dendritic channel on the face of the delta (3.36).

Bed load transport of sediment has not been well documented except in the Columbia River estuary where, although there is considerable annual variation (Jay and Good 1977), the direction of transport has been identified by the orientation of bedforms (University of Washington Department of Oceanography 1980). These studies have indicated that there is net downstream transport in most channels above Tongue Point, below which bed load transport reverses direction in response to tidal flow. The mixing region of the estuary represents a transition zone for bed load within the channel and has extremely complex bedform patterns. Tagged sediments released at the mouth of the estuary during the 1980 summer low-flow period indicated a greater (longitudinal distance) transport out of the estuary during low tidal range than into the estuary during high tidal range.

2.5.2 Chemical

Estuarine sediment chemistry can be characterized by the mineralogical and chemical composition of the sediment particles and associated interstitial detritus which, in general, can be related to the grain size structure (Burton and Liss 1976). Mineralogical composition of estuarine channel sediments is quite variable due to the different physiographic provinces (e.g., Columbia River Basin, Oregon Coast Range, Olympic Mountains, Cascade Mountains) contributing sediments to Pacific Northwest estuaries. For example, in the Columbia River, quartz, feldspar and volcanic minerals are the dominant constituents in sand particles; quartz, feldspar and mica comprise the major minerals in silt; and montmorillinite, chlorite, and kaolinite are the principal components of clay (Forster 1972). However, these constituents change dramatically along the course of the river, such that the contribution of quartz, hornblende and augite decrease downriver and volcanic rock fragments and hypersthene become more prominent below the Bonneville Dam (Whetten et al. 1969). Thus, hypersthene, clinopyroxene caugite, and hornblende characterize the sediment mineralogy of the estuary (Venkatarathnam and McManus 1973; Nittrouer 1978), although clinopyroxene at the mouth of the estuary is probably coastal-derived sediment (University of Washington Department of Oceanography 1980). Clinopyroxene also characterizes Grays Harbor sediments (Scheidegger and Phipps 1976). Kulm and Byrne (1967) recognized three distinctive suites of heavy minerals in the channel sediments of Yaquina Bay--marine, marine-fluviatile, and fluviatile. Marine sediments, characterized by pyroxenes such as diopside, and hypersthene, extend approximately 3 km into the estuary; the marine-fluviate suite occurs over approximately 6 km and is characterized by micas, muscovite, and biotite, with reduced contributions by metamorphic minerals such as kyanite, staurolite, and sillimanite; and the fluviatile suite, characterized by the micas, hematite, and limonite, occurs in the upper region of the estuary.

Organic matter in estuarine channel sediments, principally particulate organic matter (POM), originates from the excretion by animals and decomposition of plants and animals and organic particles transported into the estuary which have settled in association with inorganic (mineral) particles. A variety of measures have been utilized to quantify organic matter. Each evaluates a different spectrum of the total organic pool or its relative chemical or biological reactability. These include, but are not limited to: 1) volatile solids; 2) biochemical oxygen demand; 3) chemical oxygen demand; and, 4) total organic carbon.

Because settling of organic particles, including those resulting from flocculation processes, involves basically the same processes which determine inorganic sedimentation, the distribution of organic matter through an estuary is usually closely integrated with sediment size distribution. Exceptions to this generalization occur when point sources of organic matter (e.g., organic pollutants) within the estuary dominate local sedimentation particles. Accordingly, maximum organic content of estuarine channel sediments is usually correlated with the distribution of fine sediment particles associated with the mixing zone of the estuary, with variation due to channel bathymetry. This correlation is best illustrated by the distribution of sediment organic matter through the mainstem channel of Grays Harbor (Figs. 2.7 and 2.8). In general, peak concentrations of sediment organics occur in the inner harbor and central mixing zone portion of the estuary, particularly in association with silt and clay fractions (see Fig. 2.6). Because the channel slopes and banks have lower (integrated) water velocities than do the channel bottoms, fine organic particles have a longer period of time during which to settle there. As a result, the channel bank and slope habitats of Grays Harbor typically illustrated higher levels of organics which started occurring further up the estuary (inland) than did those of the channel bottoms.

For comparison, dredge samples of estuarine channel sediments in the Chetco River, Coos Bay, Coquille Bay, Rogue River, Siuslaw Bay, Umpqua Bay, and Yaquina Bay estuaries have had total volatile solids values ranging between 1.83-4.04%, 0.38-8.77%, 0.44-0.60%, 1.19-1.94%, 0.26- 0.61%, 0.91-3.27%, and 0.49-0.78%, respectively (Percy et al. 1974).

Estuaries may act as geochemical traps for dissolved material through flocculation and sedimentaion processes. This results in a net transfer of trace elements and organic matter to sediments (and benthic organisms), particularly in anoxic habitats where the physico-chemical conditions (e.g., redox potential) are conducive to the fixing of trace elements in estuarine sediments (Burton and Liss 1976). In general, Ni, Co, Cr, V, Ba, Sr, Pb, Zn and Y concentrations are similar in both anoxic and oxidizing sediments but Mn, Cu, Se, Zr and Mo, along with the major elements of phosphorus, carbon, and sulfur, are compatively enriched in anoxic sediments. AM Test, Inc. (1981) reported Cu in sediment elutriate from Grays Harbor as high as 1.2 mg L^{-1}; zinc as high as 1.85 mg L^{-1}; and Pb as high as 0.12 mg L^{-1}. Organic pollutants, including petroleum hydrocarbons, pesticides, PCBs (polychlorinated biphenols), and pulpmill contaminants, also tended to be more concentrated in the finer sediments adjacent to the channel. Overall, petroleum hydrocarbon concentrations as high as 5 mg L^{-1}, PCB's as high as 8.4 ppb, and pesticides (primarily aldrin and BHC compounds) as high as 4.3 ppb occurred in the elutriates from channel and adjacent sediments in the industrialized regions of the estuary.

Salinities of interstitial water in the top 6 cm of the channel sediment in the Fraser River estuary were described by Chapman (1981) as having a definite gradient structure, particularly in the mesohaline region of the estuary, and that the magnitude of the gradients changed seasonally. Maximum salinity gradation within the sediment layers was observed to coincide with the spring freshet. This suggests that sediment chemistry and infauna community structure may be influenced by this gradient structure over annual time scales, although this has not been investigated.

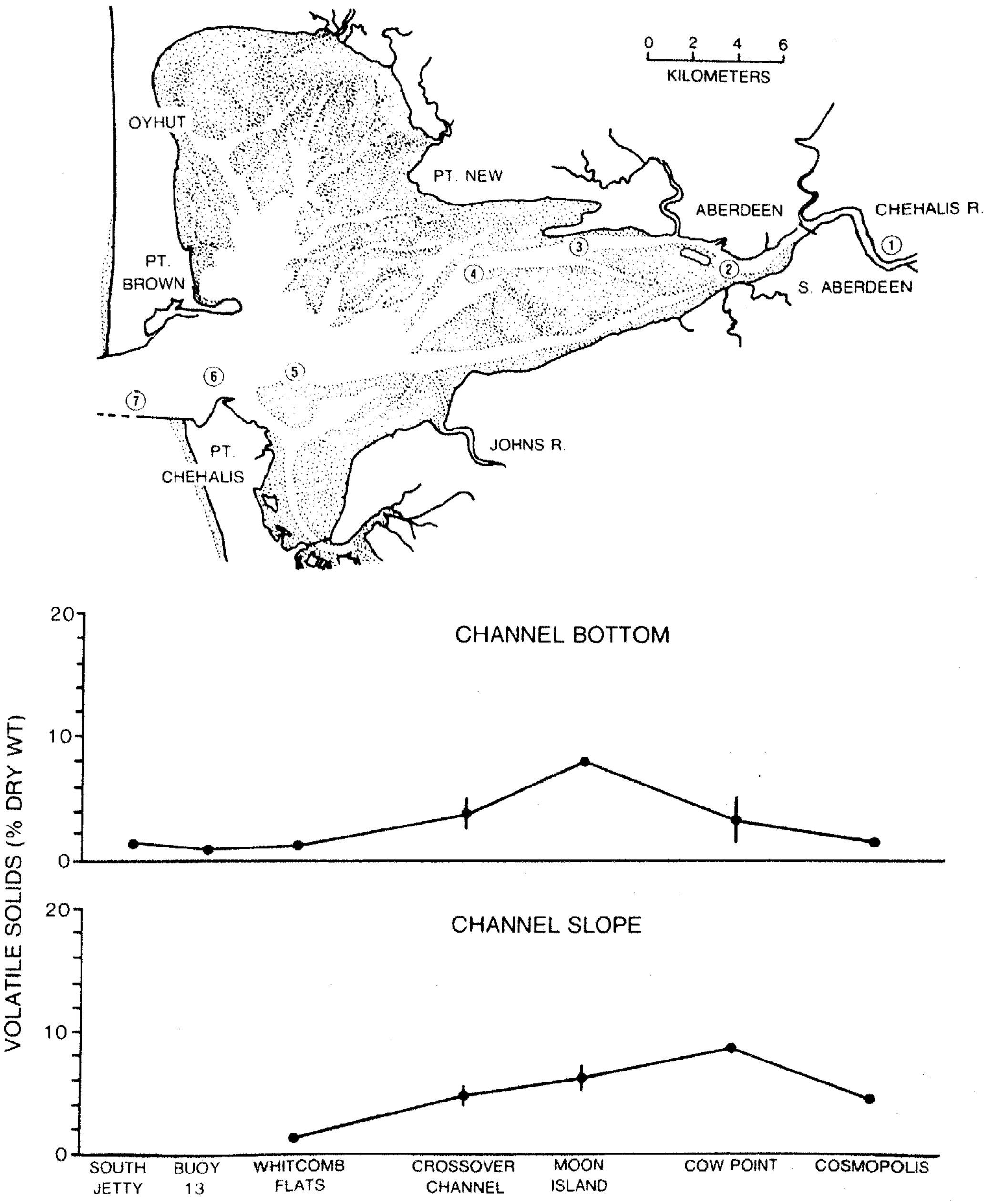

Fig. 2.7. Volatile solids (% of total dry weight) in sediments at seven channel bottom and slope locations in Grays Harbor.

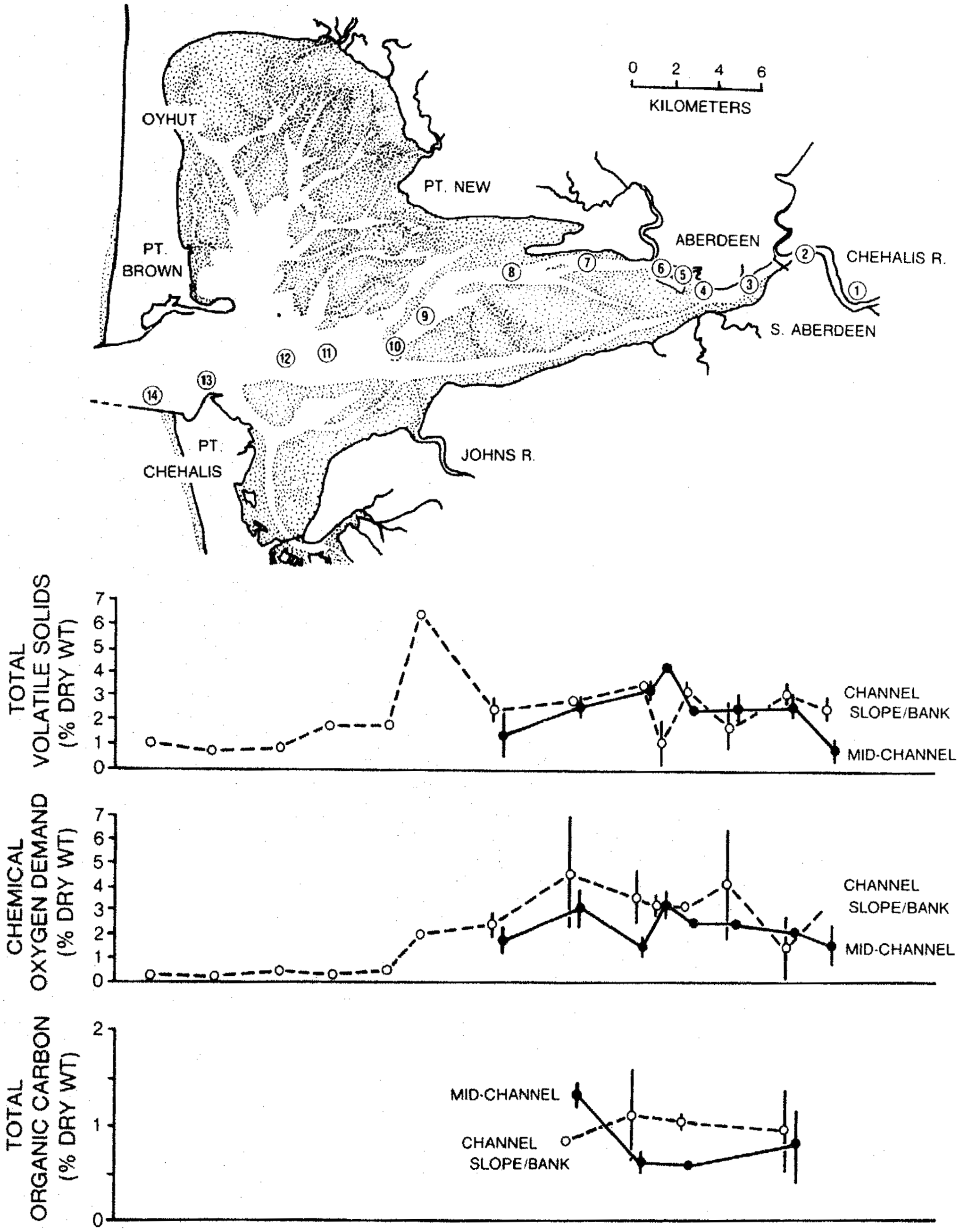

Fig. 2.8. Distribution of organic matter (volatile solids, chemical oxygen demand, and total organic carbon) in sediments at fourteen channel bottom and slope/bank locations in Grays Harbor.

2.6 ITEMIZATION AND CLASSIFICATION OF ESTUARINE CHANNEL HABITATS IN REGION

A total of 116 estuaries in the Pacific Northwest have been identified and classified according to their dominant channel habitat characteristics. Table 2.1 lists the estuaries, their extent, type, morphology, slope, and substrate characteristics for those where such information is known.

Table 2.1. Locations, characteristics, and classification of principal estuarine channel habitats in the Pacific Northwest. See text at end of table for further explanation of classification categories. Data sources included USGS (1978, 1980); Williams et al. (1975); Smith et al. (1977); U.S. Army Corps of Engineers (1976); Proctor et al. (1980); and Johnson and Gonor (1982); British Columbia data for 1981 only (Environment Canada 1982).

Estuary	Watersheds	Drainage Area (km^2)	Average Annual Discharge (hm^3 yr^{-1})	Annual Maximum Discharge (m^3 sec^{-1})	Total Extent Estuarine Area (km^2)	Estuary Type^1	Channel Morphology^2	Bank Slope^3	Substrate^4
(California)									
Eel River	Eel River	8,950	7,322	21,776					
	Salt River	-	-	-					
Humboldt Bay	Elk River	-	-	-	62	DR			
	Jacobe Creek	-	-	-					
	Freshwater Creek	-	-	-					
	Salmon Creek	-	-	-					
Mad River	Mad River	1,256	1,336	2,290					
Little River	Little River	105	126	278					
Redwood Creek	Redwood Creek	720	943	1,430					
Klamath River	Klamath River	31,400	15,568	15,800					
Smith River	Smith River	1,577	3,411	6,460					
(Oregon)									
Winchuck River	Winchuck River	181	-	-	<1	DR	F		
Chetco Bay	Chetco River	702	1,993	2,420	<1	DR	F		
Pistol River	Pistol River	-	-	-	<1	DR	F		
Rogue River	Rogue River	12,761	9,250	14,580	3	DR	F,D,B		
Elk River	Elk River	-	-	-	1	DR	F		
Sixes River	Sixes River	334	-	-	1	DR	F,B?		
Coquille Bay	Coquille River	629	960	1,660	3	DR	F,D		
Coos Bay	Coos River	1,567			50	BB	F,D,M		
	Isthmus Slough								
	South Slough								
Umpqua River	Umpqua River	9,621	6,604	7,500	28	BB	F,D,B		
Siuslaw River	Siuslaw River	107	259	86	9	BB	F,D,M		

Yachats River	Yachats River	-	-	-				
Alsea Bay	Alsea River	865	1,362	1,180	9	BB	F,D	
	Eckman Creek	-	-	-				
Yaquina Bay	Yaquina River	182	219	174	17	DR	F,D	
Siletz River	Siletz River	523	1,404	980	5	BB	F,D	
	Schooner Creek	-	-	-				
Salmon River	Salmon River	-	-	-	1	DR	F	
Neskowin Creek	Neskowin Creek	-	-	-				
Nestucca Bay	Nestucca River	834	29	25	4	BB	F,D	
	Little Nestucca Riv.							
Sand Lake	Sand Creek	44	-	-	2	BB	F,D	
Netarts Bay		36	-	-	9	BB	F,D	
Tillamook Bay	Tillamook River	1,399	1,080	1,020	**36**	BB	F,B,D	
	Wilson River							
	Miami River							
	Kilchis River							
Nehalem Bay	Nehalem River	1,728	77	1,328	9	BB	F,D,B	
Necanicum River	Necanicum River	225	-	-	1	BB	F,D?	
	Neawanna Creek							
Columbia River	Columbia River	668,200	-	-	380	DR	F,D	M-St	S
	Johns River	-	-	-					
(Washington)	Youngs River	-	-	-					
	Grays River	-	-	-					
	Lewis and Clark Riv.	-	-	-					
Willapa Bay	Bear River	60	-	21	347	BB	F,D	M-St	S-S/C
	Naselle River	142	385	315					
	South Nema River	47	-	65					
	North Nema River	56	105	55					
	Palix River	95	-	-					
	Niawiakum River	-	-	-					
	Willapa River	668	590	325					
	North River	827	860	920					
	Cedar River	33	-	-					
Grays Harbor	Elk River	47	-	-	252	DR	F,D	M-St	S
	Johns River	81	-	-					
	Chehalis River	5,358	6,670	1,570					
	Wishkah River	117	-	-					
	Hoquiam River	234	-	-					
	Humptulips River	337	1,190	935					

(continued)

Table 2.1. Continued.

Estuary	Watersheds	Drainage Area (km^2)	Average Annual Discharge (nm^3 yr^{-1})	Annual Maximum Discharge (m^3 sec^{-1})	Total Extent Estuarine Area (km^2)	Estuary Type^1	Channel Morphology^2	Bank Slope^3	Substrate^4
Copalis River	Copalis River	-	-	-		BB	M?	M	G-S
Moclips River	Moclips River	91	-	120		BB	M?	M	G-S
Quinault River	Quinault River	1,124	2,520	1,420		BB	F	M	G
Raft River	Raft River	197	-	490		BB	F?	M	G
Queets River	Queets River	1,153	3,690	3,690		BB	F	M	G
Kalaloch Creek	Kalaloch Creek	-	-	-		BB	M	M	G-S
Hoh River	Hoh River	774	2,240	1,300		BB	F	M	G-S
Goodman Creek	Goodman Creek	82	-	-					
Quillayute River	Quillayute River	1,629	-	-			F	M	G-S
Ozette River	Ozette River	229	-	45		BB	F	M	G
Mukkaw Bay	Waatch River Sooes River	33 106	- -	35 95	-				
Sail River	Sail River	14	-	20	-				
Sekiu River	Sekiu River	85	-	-	-				
Hoko River	Hoko River	113	-	3,620	-				
Clallam Bay	Clallam River	82	-	-	-				
Pysht River	Pysht River	115	-	-	-				
Lyre River	Lyre River	171	-	-	-				
Freshwater Bay	Elwha River	831	1,340	1,180	-				
New Dungeness Bay	Dungeness River	513	350	195	7*				
Discovery Bay	Snow Creek Dean Creek	- -	- -	50 -	-	F	M	M	S-S/C
Port Townsend Bay	Chimacum Creek	87	-	-	-				
Port Ludlow	Ludlow Creek	-	-	-	-	F			
Squamish Harbor	Shine Creek	-	-	-	-	F			
Thorndyke Bay	Thorndyke Creek	31	-	-	-	F			

Tarboo Bay	Tarboo Creek	32	-	-	-	F			
Jackson Cove	Marple Creek Spencer Creek	- -	- -	- -	-	F	F	M	
Quilcene Bay	Big Quilcene River Little Quilcene Riv.	- -	- -	- -		F	B	M-Sh	G-S
Dosewallips River	Dosewallips River	-	-	-	-	F	B	M-Sh	G-S
Duckabush River	Duckabush River	172	370	255	-	F	B	M-Sh	G-S
Hamma Hamma River	Hamma River	219	-	2,260	-				
Lilliwaup Bay	Lilliwaup Creek	-	-	-	-				
Annas Bay	Skokomish River	622	655	610	6				
Big Mission Creek	Big Mission Creek	-	-	-	-				
Lynch Cove	Union River	61	-	-	-				
Tahuya River	Tahuya River	-	-	-	-				
Dewatto Bay	Dewattor River	48	-	750	-	F	F,B	M	G-S
Anderson Cove	Anderson Creek	-	-	-	-	F		M	G-S
Stavis Bay	Stavis Creek	-	-	-	-	BB	F	M	G-S
Seabeck Bay	Seabeck Creek	-	-	-	-				
Little Beef Harbor	Little Beef Creek	-	-	-	-	F	F	M-Sh	S-S/C
Big Beef Harbor	Big Beef Creek	36	35	20	-	F	B	M-Sh	S-S/C
Port Gamble	Gamble Creek Miller Lake	- -	- -	- -	-				
Appletree Cove	Appletree Creek	-	-	-	-				
Miller Bay	Grovers Creek	-	-	-	-				
Liberty Bay	Dogfish Creek	-	-	-	-				
Dyes Inlet	Clear Creek Strawberry Creek Chico Creek	- - -	- - -	- - 350	-				
Sinclair Inlet	Gorst Creek	-	-	-	-				

(continued)

Table 2.1. Concluded.

Estuary	Watersheds	Drainage Area (km^2)	Average Annual Discharge (hm^3 yr^{-1})	Annual Maximum Discharge (m^3 sec^{-1})	Total Extent Estuarine Area (km^2)	Estuary Type[1]	Channel Morphology[2]	Bank Slope[3]	Substrate[4]
Olalla Bay	Olalla Creek	-	-	-	-				
Gig Harbor	Crescent Creek	-	-	-	-				
Burley Lagoon	Burley Creek	-	-	-	-				
Case Inlet	Rockey Creek	-	-	-	-				
	Coulter Creek	-	-	-	-				
	Sherwood Creek	-	-	-	-				
Hammersley Inlet	Mill Creek	-	-	-	-				
Oakland Bay	Goldsborough Creek	-	-	400	-				
Skookum Inlet	Skookum Creek	-	-	-	-				
Oyster Bay	Kennedy Creek	-	-	-	-				
Eld Inlet		-	-	-	-				
Capitol Lake	Deschutes River	417	-	3,380	-				
Henderson Inlet	Woodard Creek	-	-	-	-				
Nisqually Reach	Nisqually River	1,339	1,630	870	10*				
	McAllister Creek	-	-	-					
Chambers Bay	Chambers Creek	48	-	-	-				
Commencement Bay	Puyallup River	2,455	3,010	1,610	<0.1*				
Shilshole Bay	Cedar River	487	625	250	-				
	Lake Washington	62	50	33	-				
	Sammamish Lake	472	330	80	-				
Everett Harbor	Snohomish River	4,439	8,800	3,260	19*				
Port Susan	Stillaguamish River	1,772	2,650	1,785	24*				
Skagit Bay	Skagit River	8,011	14,900	4,080	67*				
Samish Bay	Samish River	275	-	47	15*				
Bellingham Bay	Nooksack River	2,139	3,520	1,060	13*				
Drayton Harbor	Dakota Creek	75	-	-	-				
	California Creek	59	-	-					

(British Columbia)					
Fraser River	Fraser River	218,000		8,770	
Burrard Inlet	?				
Howe Sound	Squamish River	2,330	-	2,270	-
	Mamquam River	-	-	-	-
Nanaimo River	Nanaimo River	684	-	585	-
Chemainus River	Chemainus River	355	-	416	-
Cowichan Bay	?				
Saanich Inlet					
Sooke Basin	Sooke River	-	-	-	-
	DeMamiel Creek	-	-	-	-
Muir Creek	Muir Creek	-	-	-	-
Jordan River	Jordan River	272	-	143	-
Loss Creek	Loss Creek	-	-	-	-
Sombrio River	Sombrio River	-	-	-	-
Port San Juan	San Juan River	580		943	
	Gordan River	-	-	-	-

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[1] Estuary type: DR = drowned river valleys; F = fjords; BB = bar-built; and TB = tectonic-built.
[2] Channel morphology: F = fixed; B = braided; M = meandering; and D = dendritic.
[3] Bank slope: V = vertical, 90°-45°; St = steep, 45°-30°; M = moderate, 30°-5°; and Sh = shallow, 5°-0°.
[4] Substrate: S/C = silt or clay; S = sand; G = gravel; C = cobble; B = boulder; and Cn = consolidated.

*Combined subaerial and littoral wetlands.

CHAPTER 3

PRIMARY PRODUCTION IN ESTUARINE CHANNELS

The production of plant biomass through the photosynthetic fixation of carbon occurs at several phylogenetic levels in estuarine channel habitats. This primary production is generated by both algae and true flowering plants or angiosperms. Estuarine algae, however, are a taxonomically and morphologically diverse group of flora, including epiphytic single-celled microphytobenthos and pelagic phytoplankton (i.e., diatoms, dinoflagellates), epibenthic filamentous forms, and sessile macroalgae (i.e., seaweeds, kelps). Estuarine angiosperms are usually limited to seagrasses, principally *Zostera* spp., but can also include other submerged aquatic plants such as pondweed (*Potamogeton* spp., *Zannichellia* spp.), stonewort (*Chava* sp.), *Cerabophyllum* spp., and *Elodea* spp.

3.1 BENTHIC MICROFLORA

Estuarine microflora (microscopic plants) typically includes benthic microalgae such as diatoms (Bacillariophyceae) which occur on or in the upper 1 cm of bottom sediments, although living diatoms can be found as deep as 18 cm as a result of diel vertical migration within the sediment (McLusky 1981).

Although microphytobenthos often contribute the major portion of the primary production in littoral flat habitats of Pacific Northwest estuaries, the unstable benthic environs of estuarine channel habitats would suggest that microflora assemblages are relatively limited in these habitats. Notable exceptions might be in the case of shallow blind or subsidiary channels wherein bottom sediments are more stable; unforunately, practically no information exists relative to species composition or structure of microflora in estuarine channels of this region. Pomeroy and Stockner (1976) listed five species of diatoms - *Melosira moniliformis*, *M.* cf. *nummuloides*, *Navicula cancellata*, *N. grevillei*, and *Pleurosigma zestuarii* - as dominant in the central delta region of the Squamish River estuary; *N. grevillei* was the one species noted to occur particularly in littoral flat (tidal) channel habitats from January to May.

3.2 MACROALGAE

As with the microphytobenthos, sessile macroalgae does not characteristically occur in estuarine channels due to the usual water depths and unstable, fine-textured substrates. Similarly, the notable exceptions would include shallow channels with low current velocities, i.e., blind dendritic channels on littoral flats, and channel banks with natural or artificial cobble to solid rock substrate. Macroalgae are also found attached to artificial substrates such as pilings, buoys and bulkheads.

Although not as diverse and robust an assemblage as the marine seaweeds and kelps, there are a number of estuarine macroalgae which are widely distributed and highly productive within the narrow salinity and substrate conditions they are adapted to. These generally include various blue-green algae and species of *Enteromorpha* spp. and *Fucus* sp.; in the Pacific Northwest the specific taxa are *E. clathrata* var. *crinita*, *E. intestinalis*, *E. linea* and *E. distichus*. Other less dominant euryhaline macroalgae include *Monostroma arcticum*, *E. flexuosa*, *E. minima*, *Ulva expansa*, *U. lactuca*, *Porphyra naiadum*, *Rhizoclonium riparium*, *Pylaiella littoralis*, *Vaucheria dichotoma*, and the introduced species *Sargassum muticum*. Pomeroy and Stockner (1976) indicated that *R. riparium* and *V. dichotoma* are macroalgae representative of littoral channel habitats in the Squamish River estuary.

3.3 ANGIOSPERMS

The principal taxon of angiosperms or true flowering plants common to Pacific Northwest estuaries is eelgrass, Zostera spp; this includes the principal indigenous species, Z. marina, as well as a rarer species, Z. noltii (= Z. americana). While Z. noltii occurs in only in littoral zones (Hitchock and Cronquist 1973). Z. marina occurs in sublittoral zones and, as with the benthic algae, may be found in shallow, non-mainstem channels. Substrate structure, in addition to tidal elevation and current or wave action, appears to be a principal determinant of eelgrass distribution and abundance. Although eelgrass can be found growing in substrates ranging from soft mud to gravel mixed with coarse sand, its optimum substrate composition appears to be muddy or silty sand with median grain diameters of ~250 µm (2 φ) and sorting below 500 µm (1.0 φ) (Phillips 1974). Eelgrass beds in Grays Harbor persist in habitats where fine sand (62-500 m) predominates (J.L. Smith et al. 1976). Eelgrass occurrence in Coos Bay was related to the organic content and turnover rate of sediments (Oregon State University 1977). A detailed synthesis of information on eelgrass "ecosystem" appears in Proctor et al. (1980; Section 3.2.1.3, Vol. 2).

3.4 PHYTOPLANKTON

Although perhaps not developed to the extent that phytoplankton populations in more stable, less turbid marine (e.g., oceanic) or estuarine (e.g., fjord) habitats are, phytoplankton of estuarine channels undoubtedly constitute the principal source of autotrophic production in these habitats. Three functional size groups can be said to typify phytoplankton: 1) ultraplankton, <2 µm, consisting of principally bacteria; 2) nannoplankton, 2-20 µm, consisting of small diatoms and microflagellates; and 3) microplankton, 20-200 µm, consisting of large diatoms and dinoflagellates. Although dinoflagellates are occasionally abundant (McMurray 1977) in estuaries, nannoplanktonic diatoms appear to be the most abundant forms during the summer and fall periods of peak phytoplankton production (Stockner and Cliff 1979).

Proctor et al. (1980) identified 34 taxa of diatoms as characteristic of estuarine channel habitats; of these, Chaetoceros spp., Melosira spp., and Skeletonema costatum were considered abundant, and Achnathes spp. and Lauderia spp. were considered common constituents. Karentz and McIntire (1977) listed the 42 most abundant diatom taxa in Yaquina Bay, of which Cylindroptyrxis sp., Chaetoceros subtilis, Melosira sulcata, Thalassiosira decipiens, C. socialis, C. debilis, Amphiprora paludosa, and Surinella ovata comprised more than five percent of the total cell count. Anderson (1972) described diatoms of the inshore region of the Columbia River plume as originating in part from the estuary. This assemblage was dominated by Asterionella formosa, Melosira islandica, and Thalassionema nitzschioides during the winter and by a rich flora of predominantly Asterionella japonica, Chaetoceros compressus, C. radicans, Rhizosolenia alata, R. alata gracillima, R. delicatula, and R. fragilissima during the summer. The diatom assemblage in the Columbia River estuary in April and May 1980 was found to be dominated by a relatively few freshwater species, including primarily Asterionella formosa, Melosira islandica, M. distans, Stephanodiscus hantzschii, and S. astraca var. minutula (Oregon State University School of Oceanography 1980b). The presence of uniquely marine, estuarine, or riverine phytoplankton or a combination of these assemblages within one channel location in an estuary will depend upon circulation transport and mixing of water masses, which are highly variable over short-term (tidal) and long-term (seasonal) time scales (see Section 2.3).

Dominant phytoplankton taxa during spring blooms in Burrard Inlet (Seymour River estuary with some influence from Fraser River) included Skeletonema costatum, Certaulina bergonii, and Thalassiosira spp. in the outer inlet; S. costatum and *Coscinodiscus* spp. in the inner inlet; and *S. costatum* and *Thalassiosira* spp. in Indian and Port Moody Arms (Stockner and Cliff 1979). Dominants during fall blooms were somewhat different: *C. bergonii* in the outer inlet; *S. costatum*, *Thalassiothrix* sp,. and *C. bergonii* in the inner inlet; and *C. costatum*, *nitzshcia* spp. and *Exuviella* sp. in Indian and Port Moody Arms.

3.5 ESTIMATES OF STANDING CROP AND PRIMARY PRODUCTION RATES

Two aspects are generally considered in evaluating autotrophic production: 1) the distribution of the producer biomass (standing crop) and, 2) the rate of photosynthesis. Measurements of physical and chemical parameters influencing these two variables are also documented simultaneously in order to determine the environmental factors controlling the fixation of plant carbon. Microflora and phytoplankton standing stock are typically assessed by: 1) chlorophyll *a* concentration (i.e., g cm^{-3} or mg m^{-3}); 2) particulate carbon and nitrogen (C/N); or 3) gravimetric (i.e., mg L^{-1} or mg m^{-3}) analyses. Macroalgae and angiosperm standing stock is commonly expressed in gravimetric terms (i.e., g m^{-2}). Rates of primary production of microflora and phytoplankton are generally estimated through either 1) measuring labeled carbon uptake (i.e., mg C m^{-3} hr^{-1}) during incubation at representative light levels or, 2) measuring oxygen evolution or uptake over an incubation period, which yields both production (i.e., mg C m^{-3} hr^{-1}, mg C m^{-2} hr^{-1}) and respiration rate information.

Although estimates of mean primary production of microphytobenthos as high as 108 mg C m^{-2} hr^{-1} have been documented for a littoral flat habitat in the Columbia River estuary (McIntire and Amspoker 1981), most gross primary production rate estimates in lower littoral habitats of that estuary and in Grays Harbor (Thom, unpublished) average 0.5 mg C m^{-2} hr^{-1}. Given the increased water depths, lower temperatures and unstable benthic conditions of estuarine channel substrates, it is likely that production rates in these habitats are significantly lower and more variable than are those of littoral flats. Pomeroy and Stockner (1976) described production of channel-type diatom assemblages on the Squamish River estuary as ranging between approximately 0.5 and 1.0 g C m^{-2} day^{-1}, although these were not obtained from channel habitats *per se*.

Gross primary production of estuarine macroalgae on littoral flats in Grays Harbor was found to range between approximately 1.5-2.5 g C m^{-2} hr^{-1} for *Enteromorpha clathrata* var. *crinita* (August), 1.0-1.5 g C m^{-2} hr^{-1} for *E. intestinalis* (August), 0-0.3 g C m^{-2} hr^{-1} for *E. linza* (June) and 0.5-1.0 g C m^{-2} hr^{-1} for *Fucus distichus* (June, August) (Thom, unpublished). Pomeroy and Stockner (1976) indicated that strongly euryhaline macroalgae assemblages were generally less productive (mean production of 0.6 g C m^{-2} day^{-1}) than weakly euryhaline assemblages (2.2 g C m^{-2} day^{-1}) on the Squamish River estuary delta. These production values are probably also representative of estuarine channel macroalgae which are distributed in high sublittoral elevations. Production of epiphytic macroalgae on *Zostera* blades has not been estimated but epiphytes on *Thalassia* have been estimated to equal 20% of the estimated average net production of that seagrass in Florida (Jones 1968).

Rates of primary production by eelgrass vary considerably over the temperate distribution (circumpolar) of *Zostera marina*, in part a function of the wide range in turion densities within eelgrass beds (Proctor et al. 1980) and in standing stock, which varies between 6 and 5157 g (dry) m^{-2} (McRoy and McMillan 1977). Production estimates within the Pacific Northwest region exist only for Puget Sound and range between 0.16 and 1.9 g C m^{-2} hr^{-1} (Phillips 1969, 1972).

Phytoplankton biomass and production has been systematically measured in estuarine channel habitats of only Yaquina Bay (McMurray 1977; Johnson 1981), the Columbia River (Haertel et al. 1969; Oregon State Univ. School of Oceanography

1980b), and the Fraser River estuaries (Takahashi et al. 1973; Stockner and Cliff 1979). McMurray (1977) found standing stock during the spring phytoplankton bloom in Yaquina Bay to range between 71.1 and 1.1 x 10^8 g m^{-3} and production to range between 4.7 and 172 mg C m^{-3} hr^{-1} over the same period. Johnson's (1981) studies of upper Yaquina Bay between July and November 1973 and 1974 documented an average phytoplankton standing stock of 5-6 mg m^{-3}, while maximum production of 78 to 104 mg C m^{-3} hr^{-1} occurred in July and August. Chlorophyll a measurements of phytoplankton biomass in the Columbia River estuary between April and November 1980 varied between approximately 1 and 18 mg m^{-3}, with the highest values occurring from May through July (Oregon State Univ., School of Oceanography 1980b). Higher biomass concentrations tended to occur in the upper, riverine region of the estuary and lower values in the downstream, marine region. Spatial variation indicated more homogeneity above the estuary's mixing zone region and extreme variation in or near subsidiary channels (i.e., Youngs and Lewis and Clark Rivers). Primary production measured as carbon uptake peaked at between 25 and 35 mg C m^{-3} hr^{-1} during July. Although similarly high production would have also been expected in May because of the high chlorophyll a values at that time, the eruption of Mt. St. Helens and the resulting increased inorganic suspended sediment raised the level of light extinction of phytosynthesis (see Section 3.6). Phytoplankton cells less than 10 µm, which predominate near the mouth of the estuary, and greater than 33 µm, which predominate in the upper estuary, accounted for most of the production.

Stockner and Cliff (1979) indicated that chlorophyll a generally decreased from a maximum of approximately 800 mg m^{-2} in the poorly flushed, upper reach (Port Moody Arm) of the estuary to less than 150 mg m^{-2} in the more seaward stations in outer Burrard Inlet. The fjord-type estuarine habitats of inner Burrard Inlet and Indian and Port Moody Arms showed peak primary production rates of between 4 and 6.6 g C m^{-2} day^{-1} during spring and autumn blooms, 1-2 g C m^{-2} day^{-1} in the summer interim, and essentially negligible production between November and March (Stockner and Cliff 1979).

3.6 DRIVING AND LIMITING VARIABLES TO PRIMARY PRODUCTION

A number of abiotic and biotic factors control or influence the production, distribution, and abundance of autotrophically-produced carbon, and the fate of the different micro- and macrophytic producers. These relationships are conceptually illustrated in Fig. 3.1. All producers utilize light and nutrients as the basic ingredients in assembling organic molecules, initially carbohydrates (glucose) which are transferred and transformed into amino acids, protein, and other complex molecules essential for organisms' survival, growth, and reproduction. As the universal element involved in these biological reactions, carbon is generally regarded as the most appropriate commodity to map energy flow through the ecosystem.

In addition to the photosynthetic ingredients of light and nutrients, other physical parameters such as temperature and salinity control the gross rate of biological reactions. Other environmental variables such as vertical mixing through the water column, light attenuation, substrate structure and stability, and shading regulate the magnitude and extent of solar radiation available to producers and thus ultimately affect both biomass and the rate of production by these organisms. Together, these variables are considered driving variables (ingredients or conditions limiting photosynthesis) and controlling factors (affecting the distribution of producers, primarily through physical or metabolic effects).

McIntire and Amspoker (1981) indicated that structural properties (mean grain size, skewness, sorting coefficient) of mudflat sediments in the Columbia River estuary were highly correlated

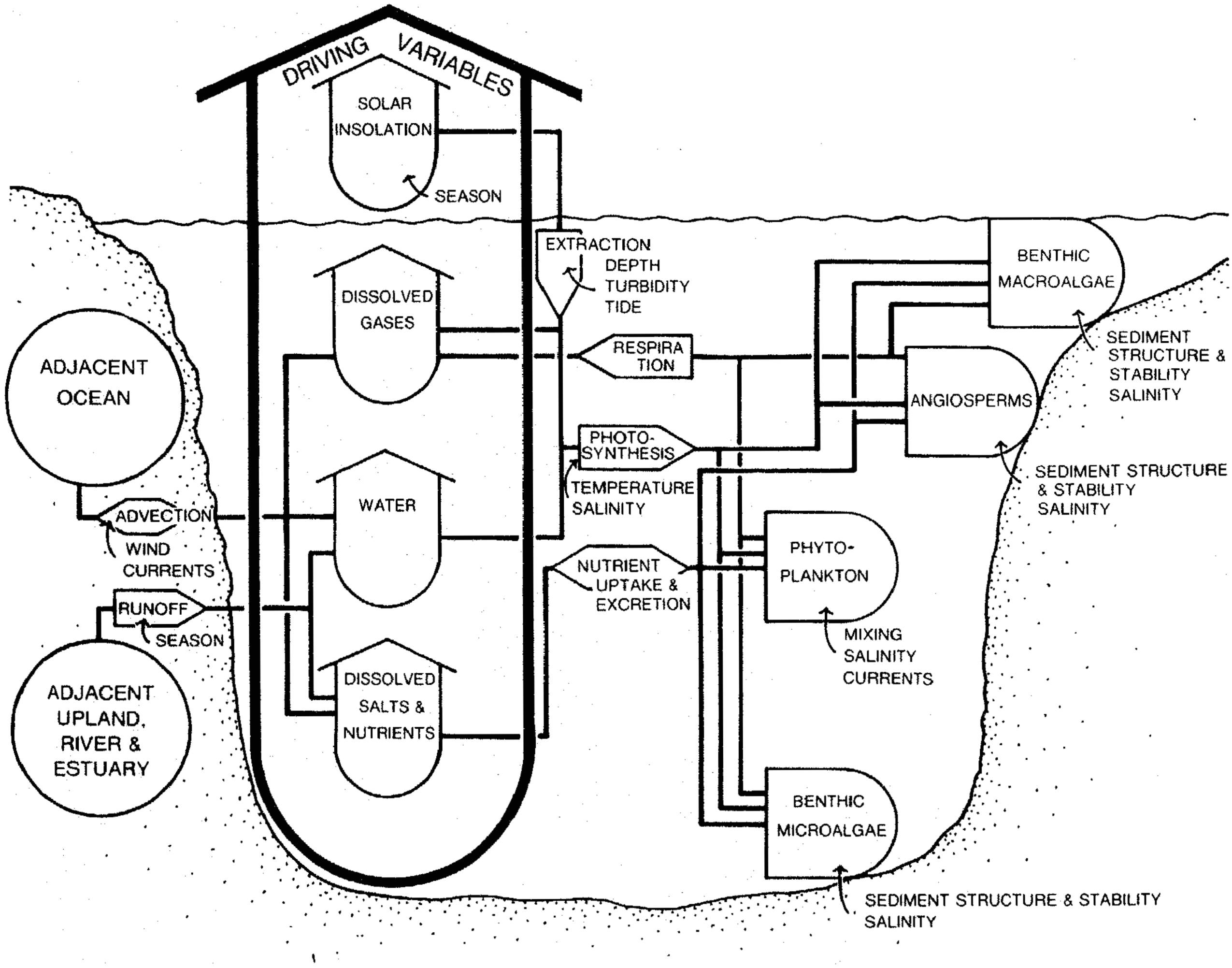

Fig. 3.1. Primary production compartments and driving variables and limiting factors influencing distribution, standing crop, and rate of production in estuarine channel habitats of the Pacific Northwest.

with the biological variables of microalgal biomass and production. The lack of any significant correlations with light intensity and temperature suggests that the microphytobenthos is highly adapted to achieve their maximum photosynthetic rate at relatively low light intensities and temperatures. Thus, substrate characteristics may be the more critical factor influencing standing crop and gross production, by regulating the ability of microalgae to colonize and persist in habitat. Welch et al. (1972) found the chlorophyll a concentrations of periphyton on submerged artificial substrates in the Duwamish River estuary directly correlated with light intensity, including that caused by increased water turbidity resulting from a rainy period. Temperature was relatively not as important a factor. The spatial distribution of periphyton, however, in the Duwamish River estuary appeared to be regulated by salinity structure.

Phytoplankton biomass distribution and production are even more affected by hydrological conditions within estuarine channel habitats due to the influences of vertical mixing of the water column. Although inorganic nutrients, particularly nitrogen, were found to be potentially limiting in late spring and summer in the Columbia River estuary, light attenuation in the water column was considerd to be of primary importance in controlling the amount of photosynthesis per unit phytoplankton biomass throughout the year (Oregon State University School of Oceanography 1980b). A simulation model of phytoplankton photosynthesis and growth in the outer reaches of the Fraser River estuary indicated that nitrate levels were limiting during the summer, that temperature was limiting production near the surface during the winter and spring, and that light was the principal limiting factor at the surface the rest of the year, and at depth throughout the year.

CHAPTER 4

DETRITUS PROCESSING IN ESTUARINE CHANNELS

In addition to the various primary producers characterizing estuarine channel habitats, described in Chapter 3, the role of organic detritus as potential sources of trophic carbon transported into and made available within the channel habitat must be considered. Recent evidence has illustrated that, directly through detritivory or indirectly through heterotrophic processes, detritus may constitute the dominant pathway of trophic carbon into estuarine food webs (Darnell 1961; Odum 1970; Qasim and Sankaranarayanan 1972; Shubnikov 1977; Correll 1978). Detritus may also have a valuable role in stabilizing estuarine systems by leveling out the seasonal variations in primary production (McLusky 1981).

Darnell (1967) has defined organic detritus as "all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species." Detritus includes both particulate and "subparticulate" matter. By the reference to microbial decomposition and utilization by consumers, this definition appears to be limited to what is commonly referred to as fine particulate organic carbon (FPOC). Since much of this material has originated from much larger organic particles which were mechanically or biochemically reduced to FPOC, this definition should be expanded to include any free (non-attached) particles of organic matter which no longer, if ever, produce carbon through photosynthesis. Included in this expanded definition, therefore, are biogenic particles of both plant and animal origin as well as free-formed (through chemical or geological processes) particles, and including associated sorbed dissolved substances and the residing microbes (Christian and Wetzel 1978).

4.1 DETRITUS SOURCES

Unfortunately, there is scant information to indicate the sources of detritus that are produced within or transported into estuarine channel habitats of the region. Thus, only speculative inferences can be made of the relative contribution of potential detritus sources.

Detritus which is usable by estuarine channel detritivores, considered to be primarily FPOC, is derived from three origins: 1) that entering the estuary already in FPOC form, previously colonized or immediately colonized by microbes once in the estuary; 2) that entering the estuary as larger particles (LPOC) and, through mechanical and microbial action, being reduced to FPOC within the estuary; and 3) that formed by the creation of organic particles (Darnell's [1967] subparticulate detritus) through the process of flocculation of dissolved organic carbon which has been either transported into or generated within the estuary (Fig. 4.1). Both particulate and dissolved carbon can enter via riverine or marine inflows or can be derived from autochthonous production within the channel or in associated estuarine habitats.

Organic particles deposited into rivers can include tree leaves and needles from forested watersheds as well as tree branches and whole tree trunks. Detrital particles indigenous to the river include phytoplankton, other (periphyton) algal cells, zooplankton exuviae and feces, and fish and other freshwater animal feces. Marine detritus includes detached macroalgae, phytoplankton cells, zooplankton exuviae and feces, and fish and other animal feces. In addition to similar macrophyte and animal sources, detritus particles

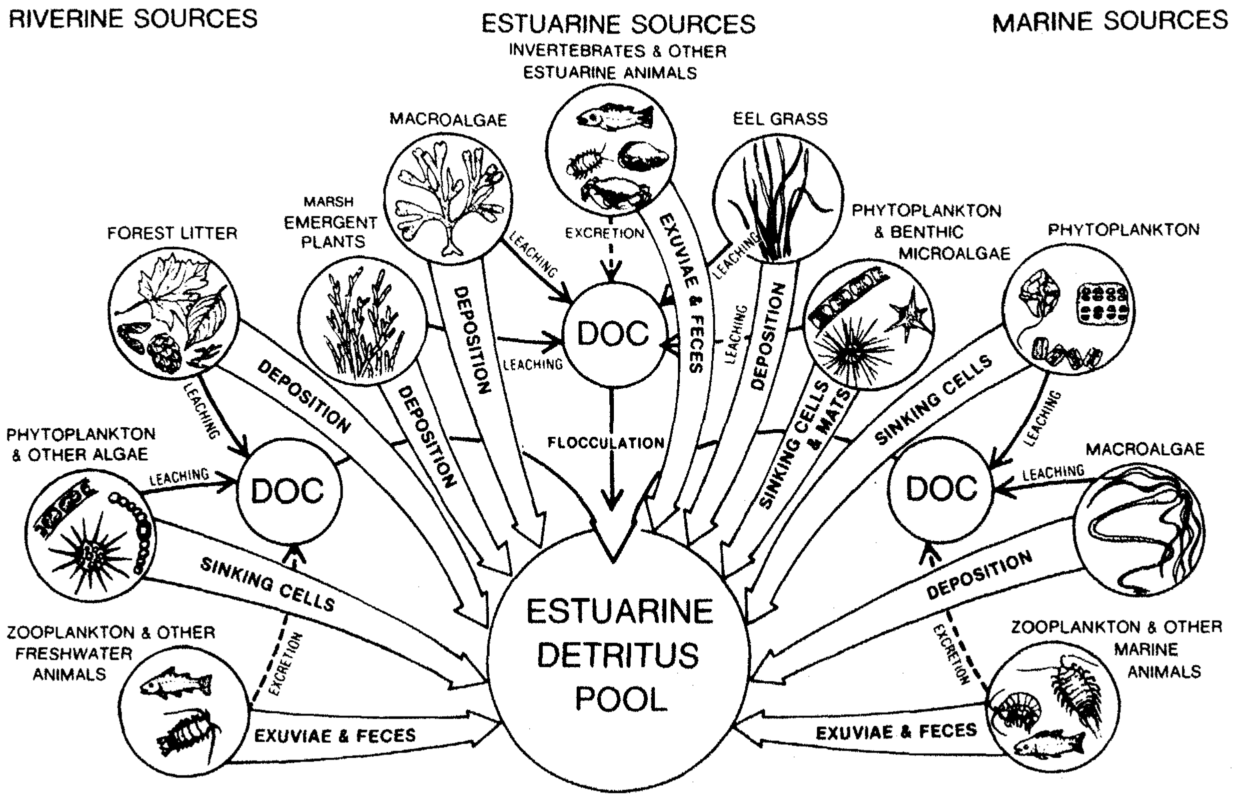

Fig. 4.1. Potential sources and pathways contributing to detritus in estuarine channel habitats of the Pacific Northwest.

produced uniquely within the estuary include abscised eelgrass blades and rhizomes and estuarine marsh plants. In addition to the influx of sinking phytoplankton cells, mats of benthic microflora established on littora flats are floated off the flats and into channel habitats during high tide cycles (C. D. McIntire and M. C. Amspoker, Oregon State Univ., unpubl. information).

Dissolved organic carbon (DOC) in rivers is considered to be primarily allochthonous, derived from the leaching of terrestrial litter, living vegetation, and soils (Fisher and Likens 1973; McDowell and Fisher 1976; Mulholland 1981); however, the contribution of autochthonous freshwater sources such as leachates from aquatic macrophytes and phytoplankton and excreta from aquatic animals has not been fully evaluated. Marine DOC, on the other hand, is essentially autochthonous, originating from leaching by zooplankton and from animal excreta; some leachates from nearshore marine algae and algal detritus may also constitute an unknown portion of marine DOC. The generation of DOC within the estuary, however, may surpass that of both riverine and marine sources due to accelerated leaching of extracellular DOC from the extensive littoral algae and saltmarsh macrophyte assemblages common to Pacific Northwest estuaries.

Leaching or excretion of DOC has also been found to be appreciable in phytoplankton and periphyton (Anita et al. 1963; Hellebust 1965, 1974; Fogg 1966, 1977) and in marine and estuarine macrophytes (Cragie and McLachlan 1964; Sieburth and Jensen 1969; Sieburth 1969; Velimirov 1980). Mann (1972) suggested that over 90% of the production of marine macrophytes enters the coastal marine food web as dissolved organic matter.

Sieburth (1969) calculated that 30% of the total carbon or 40% of the net carbon fixed daily by the littoral fucoid, Fucus vesiculosus, is exuded as DOC. Much of this exuded DOC is apparently comprised of dissolved carbohydrates, which Burney and Sieburth (1977) estimated to account for 10 to 20% of the total DOC in Narragansett Bay, Rhode Island.

Formation of FPOC from DOC through the formation of molecule masses called aggregates has been postulated as a major source of detritus in estuaries. Increased particle sedimentation results from formation of larger, denser aggregates. Aggregates from suspensions of clay and phytoplankton particles form in the presence of electrolytes such as would be encountered in estuarine mixing zones (Anvimelech et al. 1982). Although the exact mechanism of aggregate formation from DOC is not well defined, the action of bubbles rising to the water surface and bubble formation at the air-sea interface where organics tend to be highly concentrated (Harvey 1966; Goering and Wallen 1967; Williams 1967; Nishizawa 1971) appear to be important processes in creating the surface required for a particle nucleus (Ramsey 1962; Baylor and Sutcliffe 1963; Riley 1963, 1970; Sutcliffe et al. 1963; Riley et al. 1964, 1965; Krone 1978; Wallace and Duce 1978). Barber (1966) concluded that microorganisms were required in aggregate formation but the current evidence suggests that bacteria, organic, or inorganic particles can all act as the nuclei for initiating aggregation.

The formation of detrital aggregates is accelerated in estuarine channel habitats as a result of several physical and chemical processes that occur with the mixing of saline and fresh water. These processes in consort account for "salt flocculation," wherein even extremely low salinities promote the precipitation, flocculation, and aggregation of dissolved organics into organic detritus particles prone to higher settling rates (Siebruth and Jensen 1968; Gardner and Menzel 1974; Sholkowitz 1976). While it is apparent that both chemical (i.e., ionic attraction) and physical (i.e., increased particle collisions along salinity gradients) mechanisms are interrelated in flocculation (Krone 1978), no definitive work has been performed to isolate and define the functional processes of FPOC formation from DOC.

Avnimelech et al.'s (1982) experiments on the flocculation and sedimentation of algae-clay aggregates in the presence of an electrolyte suggested that increased clay concentration would promote increased flocculation and sedimentaiton of algae if the availability of aggregate nuclei is a limiting factor. This implies that flocculation of algal detritus in Pacific Northwest estuaries would be enhanced greatly during spring freshets when suspended sediment loads entering the estuaries are at a maximum.

Therefore, sources of organic detritus to estuarine channels, whether dissolved or particulate, depend upon associated terrestrial, marine, and estuarine habitats, and within the channel are the product of a number of complex and interrelated estuarine circulation and chemical processes which have not yet been successfully sorted out. Naiman and Sibert (1978) presented a seasonally-structured empirical budget of organic carbon and nutrient inputs from the Nanaimo River to the estuary and concluded that, compared to in situ primary production in the mudflat habitats, fluvial DOC (estimated to be 2 x 10^3 g C m^{-2} yr^{-1}) imported into the estuary via the river may be the greatest source of carbon to that system. Riverine input of allochthonous FPOC was estimated to equal 56 g C m^{-2} yr^{-1} and to be at least half derived from the river's periphyton community. Dahm et al. (1981) estimated that in 1974 the Columbia River exported approximately 590.4 x 10^3 metric tons of total organic carbon (TOC) of which 89% was DOC and 11% was POC; over half of the annual TOC entered the estuary between April and July, 16% of it in June. While the TOC and DOC levels were most highly correlated with river discharge, POC was correlated with primary productivity upriver.

In addition to C:N ratios (Mann 1972), lignin degradation products (Gardner and Menzel 1974; Hedges and Mann 1979; MacCubbin and Hodson 1980), and various chemical isotope characteristics used to fingerprint sources of detrital matter (Peters et al. 1978; Sweeney and Kaplan 1980; Estep and Dabrowski 1980), the ratio of two stable carbon isotopes, C^{13}/C^{12} (abbreviated as $\delta^{13}C$), has recently been utilized to identify the possible origins of organic carbon present in consumer organisms. This is possible because the ^{13}C values of an animal's tissues are usually unaltered from those of the carbon in its food source (DeNiro and Epstein 1978; Teeri and Schoeller 1979). This approach has been used, apparently successfully, in documenting the importance of various carbon sources to estuarine and marine detritivores (Thayer et al. 1978; Haines and Montague 1979; McConnaughey and McRoy 1979; Fry 1981). Using lignin oxidation products in conjunction with $\delta^{13}C$, Hedges and Mann (1979) indicated that the POC from the Columbia River deposited in offshore sediments was dominated by gymnosperm woods and non-woody angiosperm tissues.

Using ^{14}C-labelling techniques, Sibert et al. (1977b) amassed evidence that the production of detritivorous harpacticoid copepods in the Nanaimo River estuary (see Section 5.3) was supported predominantly by the bacterial flora associated with organic detritus which was presumed to originate from several exogenous and endogenous sources, including: (1) meadows form the seaward areas (2) algae from intertidal areas; (3) saltmarsh plants from landward areas; and (4) downstream transport from the upland areas of the estuary's watershed. In their recent $\delta^{13}C$ studies of detritus-based food webs in Hood Canal, Wissmar and Simenstad (Fish. Res. Inst., Univ. Wash., unpubl. data) have found the detritus sources to vary seasonally, with shifting contributions of riverine, marine and endemic estuarine-produced carbon. At the same time, a considerable recycling of autochthonous carbon within the estuary was a prominent characteristic of the detritivore component of the estuarine food web.

4.2 DISTRIBUTION OF DETRITUS

Very little information exists on the deposition, distribution and flux of detritus in estuarine channels, and virtually none exists for the Pacific Northwest. Pickral and Odum (1976) found that the non-uniform distribution of detritus in a Virginia saltmarsh tidal creek related to the morphology and hydraulic regime of the creek. They deduced that detritus particles, hydrodynamically equivalent to fine sand and silt particles, tended to accumulate in low velocity zones inside meanders and behind sills; storm events, however, were responsible for periodically flushing detritus accumulations from the tidal creek.

The flux of detrital particles within channels probably occurs in conjunction with the sediment bedload and is influenced by similar factors (Section 2.5.1). Accordingly, variations in boundary layer velocities determine the size distribution, flux, and accumulation of detritus particles through channels. Depositional regions, where current velocities are lowest, would be expected regions of detritus accumulation. This is observed in blind or subsidiary channels with lower velocity regimes which tend to accumulate more detritus than do mainstem channels.

But, as with suspended inorganic particles, the mainstem channels in mixing or entrapment zones of estuaries also probably constitute locations of maximum settling of organic particles and inorganic-organic particle aggregates. Although the long-term net transport is probably seaward, detritus particles may remain within this zone for periods long enough to be extensively utilized by detritivores. Naiman and Sibert (1978) pointed out the importance of "retention structures" as traps of organic detritus, and identified oyster beds, macroalgae, and spaces around cobbles as FPOC retention structures and logs and eelgrass as LPOC retention structures. To this list should also be added the emergent plant assemblages of estuarine salt marshes. They concluded that fjord and drowned river valley estuaries, with little oceanic exchange, large areas, and numerous types of retention structures may be the most efficient retainers of allochthonous detritus.

4.3 FUNGI AND BACTERIA COLONIZATION

Microorganisms, primarily bacteria, fungi, and protozoa, rapidly colonize fresh detritus particles and are largely responsible for conditioning detritus to the stage where it is physically and nutritionally viable for consumption by detritivores and other primary consumers (Fenchel and Jørgensen 1977). Harrison and Harrison (1980) indicated that in microcosm experiments, fresh *Zostera marina* blades supported a two-week bloom of suspended bacteria. They also found that fresh detritus had 100 x 10^3 bacteria cells mm^{-2} while aged detritus had only 20-40 x 10^3 cells mm^{-2}. Colonization by microalgae (pennate diatoms, flagellated prasinophytes, and filamentous blue-greens), however, tended to be inversely related to bacteria density when inorganic nutrients were limiting, suggesting that either the two groups were competing for the available nutrients or that one or the other was producing inhibitory substances (Delucca and McCracken 1977).

Stuart et al. (1981) conducted controlled experiments of heterotrophic utilization of particulate (43-63 µm) kelp debris and found that maximum bacteria biomass ($\sim$4 mg l^{-1}) occurred within ten days; thereafter, phagotrophic flagellates, ciliates, amoebae, and choanoflagellates successively dominated the microbial community. During the initial two days of the experiment dissolved organics from the particles were used by free-living bacteria. Over the next four days there was rapid growth of the bacteria population attached to the particles, with substrate carbon converted to bacterial biomass at a conversion efficiency of about 33%. The following four days, until grazing flagellates appeared, were characterized by a rapid decline in the rate of bacterial growth, with a drop in the conversion efficiency of approximately 10-11% as only particulate carbon was utilized.

We generally know very little about the microbial assemblages characterizing Pacific Northwest estuarine channels, although Wiebe and Liston (1972) included estuarine channel samples in their analyses of aerobic, nonexacting, heterotrophic benthic bacteria of the Washington and Oregon coasts. The highest individual counts ($\bar{x} = 55{,}925.9 \pm 23.7$ viable counts bacteria ml^{-1} of mud-water slurry) were documented from the sandy sediments at Harrington Point in the Columbia River estuary but were much more variable than those in sediments beyond the influence of the Columbia River. Qualitatively, three groups of *Pseudomonas* strains, all nonpigmented carbohydrate utilizers (Shewan 1963), comprised 85% of the bacteria isolates identified in the estuary; the only significant non-*Pseudomonas* strain found was *Achromobacter*, a nonpigmented, nonmotile rod form. Cellulose-digesting bacteria were relatively unique to estuarine and continental shelf sediments.

4.4 PHYSICAL, CHEMICAL, AND BIOLOGICAL CONDITIONING

Undoubtedly one of the most critical rate-controlling processes in the detritus pathway of an estuarine food web is the conversion of detritus to particles of physical dimensions and nutritional character which can be utilized by detritivores. This process, termed "conditioning" of the detritus, involves physical, chemical, and biological mechanisms (Fig. 4.2). Physical and chemical decay are due primarily to the weathering of the larger component of LPOC particles through leaching and autolysis of soluble or volatile material. Physical conditioning also includes the mechanical breakdown of cell walls by wind, wave, and current action, which increases the rate of chemical decay. This is particularly evident in exposed, coarse substrate (e.g., cobble) littoral habitats, where continued sediment movement acts to break loose macrophyte material into progressively finer particles (Fig. 4.3).

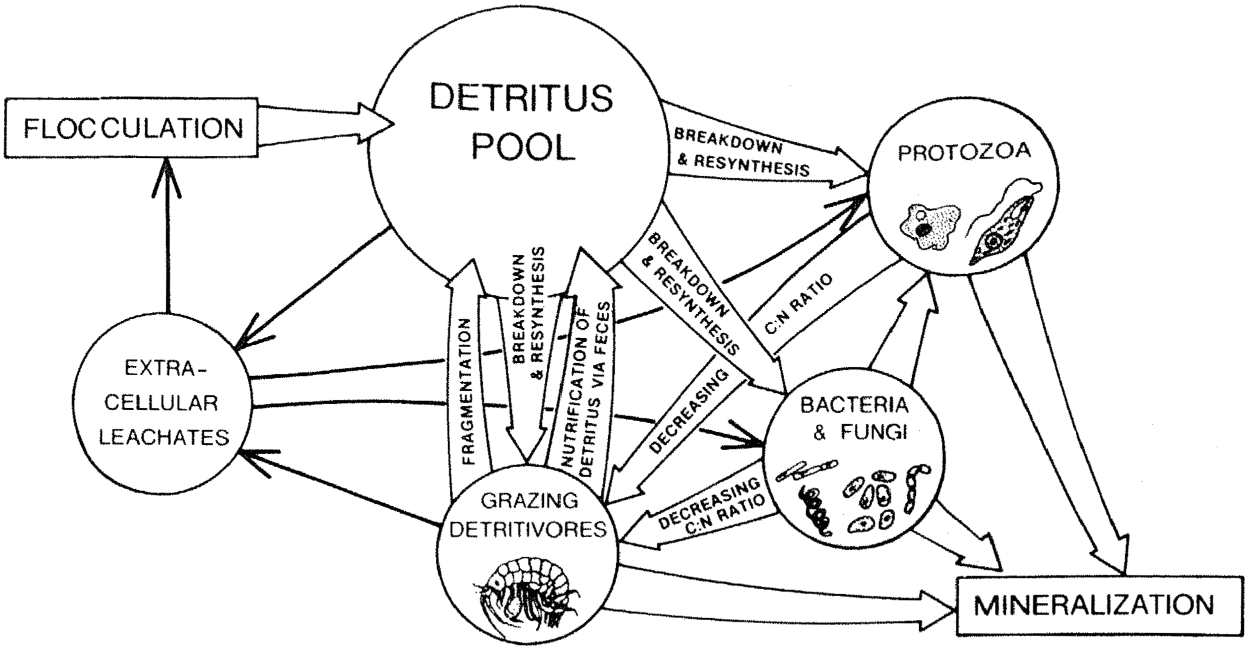

Fig. 4.2. Conceptual illustration of the mechanisms and flows involved in the physical, chemical, and biological conditioning of detritus.

Fig. 4.3. Terrestrial (wood chips, tree bark, and leaves) detritus of varying particle sizes deposited on littoral flats of Duckabush River estuary, Hood Canal, Washington; once degraded into finer particulate matter by physical processes, the fine particulate detritus is transported into blind or subsidiary channels where further biological and chemical degradation and, ultimately, utilization take place (photo by author).

Litterbag experiments, wherein fresh (live) macrophytes are placed in mesh bags and secured in littoral or marsh habitats for temporal monitoring of decomposition, have often been used to document the breakdown of large detritus. Kistritz and Yesaki (1979) followed the disappearance of the sedge, Carex lyngbyei, in the Fraser River estuary. They found that 40% of the ash-free dry weight remained after approximately nine months (September-June) and that decay was most precipitous during February due to increased physical deterioration and tidal removal. Science Applications, Inc. and Woodward-Clyde Consultants (1981) conducted litterbag experiments using seven emergent plant species (Carex lyngbyei, Potentilla pacifica, Agrostis alba, Juncus balticus, Scirpus validus, Deschampsia cespitosa, Triglochin maritimum) characteristic of the Columbia River estuary. They found varying rates of decomposition with plant species, locations in the estuary, and tidal elevations, with rates varying from 6% to 51% over five months. Rates were typically higher in the riverine portion of the estuary and succulent marsh plants generally decomposed more rapidly than did grasses.

As much as 89% of the biomass of particulate kelp detritus incubated in Stuart et al.'s (1981) experiments was lost in 30 days and the maximum loss occurred in the initial 14-18 days. This experiment was conducted in the absence of any herbivorous organisms, which by their own fragmentation and ingestion of detrital particles accelerate the decomposition by increasing the surface area available for microbial colonization. Herbivores also increase the nutritional quality of the detritus pool through the addition of nitrogen in their feces particles (Fig. 4.2).

Most consumers require food sources with an average ratio of carbon to nitrogen <17 to avoid protein deficiency (Russel-Hunter 1970). The initially high carbon:nitrogen ratio of detritus is lowered through the production of proteins and utilization of carbohydrates by decomposers (Mann 1972) so that the detritus becomes usable by detritivorous consumers. Thus, the recycling of POC through the decomposer-detritivore phase of an estuarine food web (see Chap. 9) promotes the availability, quality, and transfer of detrital carbon into the food web.

Biological conditioning of detritus involves fragmentation of LPOC by the grazing action of animals (Harrison and Mann 1975) and the microbial degradation of FPOC. Since the rate of leaching and microbial degradation increases with decreasing particle size (Harrison and Mann 1975; Fenchel 1977), biological fragmentation may be an important rate-limiting process to detritus conditioning, especially in the case of seagrass-based detritus (Robertson and Mann 1980).

In other regions, epibenthic herbivorous crustaceans, including isopods and gammarid amphipods, have been shown to be particularly important in reducing detritus particle size, producing additional, smaller detritus particles in the form of feces, and excreting nitrogen-rich materials which enhance microbial decomposition (Fenchel 1970; Lopez et al. 1977; Harrison 1977; Robertson and Mann 1980). Although there have not been any related investigations in this region, the high densities of epibenthic crustaceans in Pacific Northwest estuarine channels (see Section 5.3) would suggest that this is also an important process in detritus conditioning in these habitats. Griffiths and Stenton-Dozey (1981) estimated that between 60% and 80% of the kelp debris deposited in the littoral zone of a South African beach was consumed by amphipods and dipteran larvae within 14 days of deposition. The proportion of this detritus and the byproducts of the consumer organisms which entered the nearshore marine food web as detritus fragments, feces, exuviae, and DOC is unknown; the authors noted, however, that significant export of such material was evident during high spring tides.

Despite the recent focus upon the dynamics of the detritus-microbe complex, it is readily apparent that interactions between detrital substrates, decomposer microbes, and their consumers in estuaries are more complex than realized initially (Christian and Wetzel 1978). As such, the relative importance of energy and nutrient requirements of microbes and consumers, the heterogeneity of microbe colonization in time and space, and the magnitude and pathways of nutrient and carbon recycling within the decomposer-detritivore phase of the estuarine food web must be further defined for different detritus sources as well as within the various estuarine habitats such as channels.

CHAPTER 5

INVERTEBRATE ASSEMBLAGES OF ESTUARINE CHANNELS

Invertebrate animals characteristic of estuarine channel habitats are typically categorized by size, microhabitat, and life history characteristics. Size categories include:

1. Meiofauna; animals 100 to 500 µm, including primarily foraminiferans, nematodes, kinorhynchs, ostracods, harpacticoid copepods, turbellarians, oligochaetes, halacarids, gastrotichs, and cephalocarideans; and
2. Macro- or megafauna; animals larger than 500 µm, including primarly polychaetes, calanoid and cyclopoid copepods, leptostracans, mysids, cumaceans, tanaids, isopods, amphipods, euphausiids, decapods, gastropods, pelecypods, and echinoderms (Mare 1942; Carriker 1967).

Microhabitat categories include:

1. Benthic infauna; animals inhabiting the sediment, either beneath or in the surface of the bottom substrate;
2. Sessile epifauna; animals relatively permanently attached to the substrate;
3. Motile epifauna; animals which actively move about on the bottom;
4. Epibenthic zooplankton; semiplanktonic animals inhabiting the interface between the substrate and water column, either passively or actively moving between the very surface layer of the substrate and the boundary layer of the water column; because of the emergence of many motile infaunal organisms from the benthos, there often is overlap between the benthic infauna and epibenthic zooplankton assemblages;
5. Pelagic zooplankton; planktonic animals inhabiting the water column; and,
6. Neuston; animals drifting upon or immediately associated with the surface layer of the water column.

Life history categories refer primarily to planktonic animals and include:

1. Meroplankton; temporarily planktonic animals, usually eggs and larvae of benthic and nektonic adults; and,
2. Holoplankton; permanently planktonic animals which live in the water column throughout their complete life cycle (Sverdrup et al. 1942).

While the following description of estuarine channel invertebrate assemblages is organized along microhabitat categories, these other descriptors will further categorize invertebrate fauna within their microhabitats. Inclusion of characteristic organisms in unique microhabitat categories, furthermore, is often complicated by the behavior of animals and of the scientific apparatuses used to sample them. Therefore, the following descriptions of invertebrate assemblages are functional, in that animals are included according to their occurrence in the reported collections, even though their microhabitat distribution may be poorly represented and considerable overlap is evident.

5.1 BENTHIC INFAUNA AND SESSILE EPIFAUNA

Due to their permanency within or upon estuarine channel substrates, benthic infauna and sessile epifauna are the assemblages most structured by variations and gradients in physical and chemical characteristics of the benthic environs of the estuary. But, on the other hand, they exhibit the most stable structures over time due to the assemblage's adaptation to highly variable conditions.

The two factors most often cited as structuring the distribution of estuarine benthic infauna are salinity and sediment structure (Wieser 1959; Gunter 1961, Carriker 1967; Gray 1974), especially given their typical longitudinal gradient structure through most estuaries. Associated physical and chemical factors such as sediment stability and organic content constitute related influences which cannot necessarily be separated from sediment grain size and texture (Sanders 1959). The same holds for biological factors such as competition, predation, and life history cycles (Peterson 1979). But in general, and especially in the more dynamic channel habitats, estuarine hydrology is the underlying, composite factor determining the distribution of benthic infauna through the structuring of salinity, sediment, velocity, and organic matter.

The role of salinity in mainstem channels has not often been correlated to the distribution of benthic infauna in Pacific Northwest estuaries. Marriage (1954) and Burt and McAlister (1958) illustrated that the gaper clam, Tresus capax, and softshell clam, Mya arenaria, were distributed in salinity zones greater than 25°/oo between 20°/oo and 0°/oo, respectively.

Benthic infaunal assemblages of the Columbia River estuary have been sampled extensively (Columbia River Estuary Data Development Program [CREDDP] 1980), particularly in reference to the effects of dredging and dredge-material disposal within and immediately adjacent to the estuary (Sanborn 1975; Higley et al. 1976; Durkin et al. 1979; Higley and Holton 1978; Blahm 1979). It was not until the initiation of the CREDDP studies that detailed synoptic and ecological investigations of benthic infaunal assemblages were conducted throughout the estuary (Oregon State University School of Oceanography 1980a). At the initiation of the CREDDP studies, a composite species checklist of the estuary's infauna included 212 taxa; 23% of which were polychaete annelids; 14% gammarid amphipods; 9% bivalve molluscs; and 8% each, gastropod molluscs and isopods (VTN, unpublished, cited in Oregon State University School of Oceanography 1980a).

Unfortunately, only a few of the CREDDP benthic infauna sampling stations are located in channel habitats and information from these stations is as yet incomplete. However, the combined studies of the Columbia River estuary, culminating with the on-going CREDDP research, still present the most comprehensive illustration of benthic infauna in estuarine channel habitats of the region (Fox 1981).

A diverse, low standing stock, infaunal assemblage typifies the region at and immediately within the mouth of the Columbia River estuary in a benthic environment characterized by large-grained, unstable sand substrate of low organic content and high salinities. While no true channel habitats have been sampled, sampling in closely adjacent sampling sites suggest that nemerteans, nematodes, oligochaetes, polychaete annelids (Magelona spp., Capitella capitata, Paraonella platysvanchia, Eteone spp., Nephthys californiensis, Haploscoloplos spp., Spio filicornis, Spionidae spp.), gammarid amphipods (Phoxocephalidae spp., including Araphoxus milleri, and P. stenodes, Eohaustories estuarius, E. washingtonianus, Synchelidium shoemakeri), and bivalve molluscs (Macoma balthica are the dominant infauna within channels); total density of the assemblage ranges between 200 to 1000 individuals m^{-2} (Higley and Holton 1978; Oregon State University School of Oceanography 1980a; R. Holton and D. Higley, Oregon State University, unpublished CREDDP data).

Benthic infauna in the central region and principal mixing zone of the Columbia River estuary illustrate extreme spatial and temporal variability, even within distinguishable habitats such as the channels. As described in Chapter 2, salinities are highly variable (5‰-25‰) and the sediment (medium sand) prone to resuspension and differential, active transport. Gammarid amphipods (Corophium salmonis, Eogammarus confervicolus, E. estuarius), oligochaetes, polychaete annelids (Glycinde armigera, Magelona sacculata, Polydora sp., Paraonella platybranchia, Hobsonia florida, Neanthes sp.), and cumaceans (Hemileucon spp.) dominate the infaunal assemblage within or closely adjacent to channels, and the total assemblage can sustain high densities (20,000-70,000 m^{-2}; Higley et al. 1976; R. Holton and D. Higley, Oregon State Univ., unpublished CREDDP data).

The benthic infauna assemblage of the subsidiary channel entering the mixing zone region from the Lewis and Clark and the Youngs Rivers through Youngs Bay best illustrates the synergistic influence of the fine sediments (fine sand to coarse silt) and high sediment organics, despite relatively high current velocity regimes (Boley et al. 1975). Tube-building gammarid amphipods (C. salmonis), polychaete annelids (H. florida, Neanthes limnicola), bivalve molluscs (M. balthica, Carbicula manilensis), oligochaetes, and chironimid larvae dominated the finer substrates. Oligochaetes dominated numerically over Corophium in the very fine, highly-organic sediments and other amphipods (E. estuaris, Anisogammarus marus sp., Paraphoxus sp.) replaced Corophium in the coarser, less organic sediments closer to the mainstem channel in the central portion of the estuary (Higley and Holton 1975). Total densities of benthic infauna in the inner-bay channels exceeded 30,000 m^{-2} but were only 323 m^{-2} in the outer-bay portion of the channel (Higley and Holton 1975). Specifically, C. salmonis occurred in densities between 19,000 and 29,000 m^{-2}; oligochaetes, in densities between 5,000 and 33,000 m^{-2}; and polychaetes, between 600 and 2,200 m^{-2} in the fine sediment channel bottom habitats.

Channels in the upper estuarine and riverine regions of the estuary include both the mainstem, navigation channel and subsidiary channels in the complex island-tidal marsh habitats where salinities are low to absent and sediments are typically coarse (medium sand). Gammarid amphipods (C. salmonis, Monoculodes spinipes, Phoxocephalidae spp.), polychaete annelids (N. limnicola), oligochaetes, bivalve molluscs (C. manilensis), and chironomid larvae are representative benthic organisms in this region. Total densities tend to be low, <1,000 m^{-2}, in both mainstem and subsidiary channels; amphipods occur in densities < 50 m^{-2}, oligochaetes < 20 m^{-2}.

Although similar information from estuarine channels of other coastal estuaries is not available, the available data on the Rogue River (Rattie 1979b), Coos Bay (Roye 1979), and Netarts (Kreag 1979a) estuaries indicates that, with a few exceptions, the Columbia River estuary's infauna assemblages are representative (Fig. 5.1, Table 5.1). Boyce (1979) found large populations of Corophium spinicorne and Eogrammarus (Anisogammarus) confervicolus in channel habitats of the Rogue River estuary. Stout (1976) and Gaumer et al. (1978) described the bivalve molluscs, Saxidomus giganteus, Tresus capax, T. nuttallii, Zirfaea pilsbryi, Penitella penita, and Clinocardium nuttallii, as being distributed in the subsidiary channels of Netarts Bay; S. giganteus was unique to the marine portion of the channel and C. nuttallii was unique to the mid- and upper-bay portion. Slotta et al. (1973), Parr (1974), Jefferts (1977), and Gaumer (1978) have described the infauna of the dredged navigation channel in Coos Bay. Gaumer's (1978) distributional surveys of economically important bivalves (maps reproduced in Roye 1979) indicate that, although the highest densities occur in littoral zones, T. capax, C. nuttallii, Macoma spp., and P. staminea are also common on the slopes of the channel in the lower, marine portion of Coos Bay. Parr (1974) and Jefferts (1977) presented evidence that the infauna assemblage in the downstream channel was more diverse than in the estuarine, upper channel. Parr attributed this diversity to the maintenance of an assemblage of pioneer species (such as the polychaete annelid Streblospio benedicti) in the

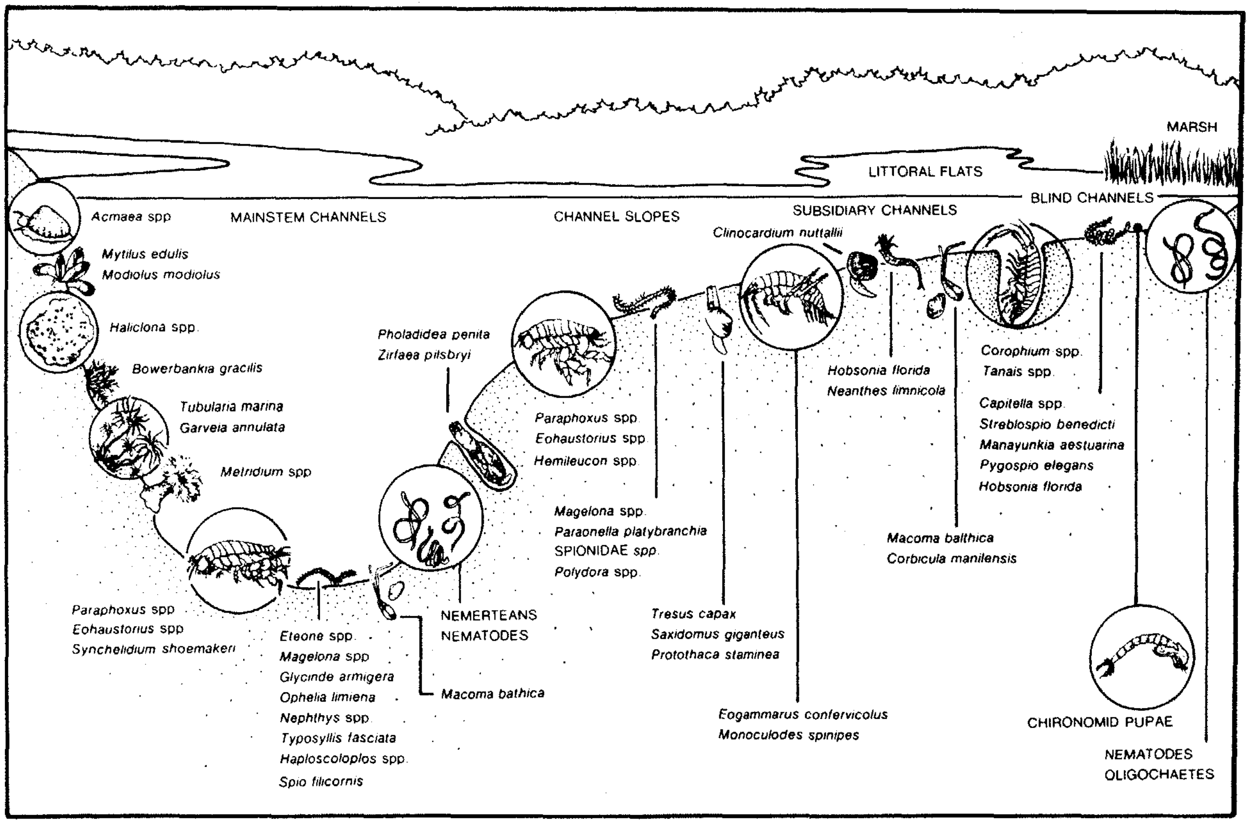

Fig. 5.1. Representative illustration of common benthic infauna and sessile epifauna assemblages of estuarine channel habitats of the Pacific Northwest.

frequently dredged channels in the upstream portion of the estuary. Elsewhere, channel habitats have been studied on a more limited basis. Mainstem channels in the lower, marine-influenced region of Coos Bay, Oregon are characterized by coarse-grained, ocean-derived sand in the bottom sediments and steep, mudstone walls where a navigation channel was created. The unconsolidated bottom sediments are characterized by the polychaete annelids Ophelia limiena, Nephthys spp., and Typosyllis fasciata, while the consolidated mudstone walls harbor burrowing pelecypods or piddocks, Pholadidea (Penitella) Penita (Jefferts 1977; Hancock et al. 1977). Sessile organisms on the channel wall include the mussels Mytilus edulis and Modiolus modiolus; encrusting sponges, Haliclona spp.; bryzoans, Bowerbankia sp.; hydroids, Tubularia marina; and the anemone, Metridium sp. (U.S. Dep. Interior 1971). The polychaete annelid, Glycinde armigera, and gaper clam, Tresus capax, were the predominant infaunal macroinvertebrates in the less-scoured channel bottom of the South Slough portion of Coos Bay (Hancock et al. 1977).

Undoubtedly the most complete quantitative characterization of benthic infauna in dendritic channels of estuarine salt marshes (tidal creeks) in the region is that of Siletz and Netarts Bays, Oregon by Higley and Holton (1981). They found that oligochaetes numerically dominated the macroinvertebrate assemblage, accounting for approximately 50% and 70% in mature high marsh and sedge marsh tidal channels, respectively; polychaete annelids and amphipods often accounted for over 10%, and nematodes, dipteran larvae, cumaceans, and harpacticoid copepods were somewhat less abundant.

Table 5.1. Itemization and characteristics of benthic infauna and sessile epifauna common to estuarine channel habitats of the Pacific Northwest.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Sediment Associations[3]	Relevant Life History Characteristics
PORIFERA				
Haliclona sp.	M	E,P	Cn	
HYDROIDA				
Garveia annulata	M	E,P	Cn	
Tubularia marina	M	E,P	Cn	
ANTHOZOA				
Metridium spp.	M	E,P	Cn	
BRYOZOA				
Bowerbankia gracilis	M	E,P	Cn	
NEMERTEA	M,S,B	R-E	SC,S,G	
NEMATODA	S,B	R-E	SC,S,G	
OLIGOCHAETE ANNELIDS	S,B	R-E	SC,S	
POLYCHAETE ANNELIDS				
Capitella spp.	M,S,B,	O-P	SC,S	
Typosyllis fasciata	M,S	E,P	S,G	
Neanthes limnicola	S	O-P	SC,S	
Nephthys californiensis	M,S	E,P	S,G	
Eteone spp.	M,S	E,P	S	
Glycinde armigera	M,S	M-P	S	
SPIONIDAE SPP.				
Pygospio elegans	B	M-P	S	
Streblospio spp.	S,B	M-P	S	
Spio filicornis	M,S	E,P	S	
Haploscoloplos spp.	M,S	E,P	S	
Polydora spp.	S	P	S	
Magelona spp.	S	E,P	S	
Ophelia limiena	M,S	E,P	S,G	
Hobsonia florida	S,B	P	S	
Paronella platybranchia	M	E,P	S	
Manayunkia aestuarina	B	M-P	S	
GASTROPOD MOLLUSCS				
Acmaea spp.	M	E,P	Cn	
BIVALVE MOLLUSCS				
Mytilus edulis	M	E,P	Cn	

(continued)

Table 5.1 Concluded.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Sediment Associations[3]	Relevant Life History Characteristics
BIVALVE MOLLUSCS - cont'd.				
Modiolus modiolus	M	E,P	Cn	
Macoma balthica	M,S,B	E,P	SC,S	
Crobicula manilensis	S,B	R-O	SC,S	
Protothaca staminea	M,S	E,P	G	
Saxidomus giganteus	M,S	E,P	G	
Tresus capax	M,S	E,P	Cn	
Pholadidea penita	M,S	E,P	Cn	
Zirfaea pislbryi	M	E,P	Cn	
Clinocardium nuttallii	S	M-E	S,G	
TANAIDS				
Tanais sp.	B	M-P	S	
GAMMARID AMPHIPODS				
Amphithoe spp.	S,B	R-P	SC,S	
Corophium spp.	S,B	R-P	SC,S	Tube-dwellers
Anisogrammarus sp.	S	M-P	SC,S	
Eogammarus confervicolus	M,S	P	S	
Eohaustorius estuarius	M,S	M-E	S	
Monoculodes spinipes	S	O-M	S	
Phoxocephalidae	M	O-E	S	
Paraphoxus spp.	M,S	E,P	S	
DIPTERAN INSECTS				
Chironomidae	B	R-P	Sc	Larvae, pupae

[1] M = mainstem; S = subsidiary; B = blind.

[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline.

[3] SC = silt/clay; S = sand; G = gravel; C = cobble; B = boulder; Cn = consolidated.

Among the amphipods, *Corophium* spp. comprised about 90% of the total number in both marshes, with *Anisogammarus confervicolus* contributing up to 10% in the sedge marsh and talitrids and *Amphithoe* spp. also occurring in the mature high marsh. Capitellids accounted for most (59%-75%) of the numbers of polychaetes in both marsh habitats, but *Hobsonia florida* was also prevalent (>20%) in the sedge marsh channel, and ampharetids, spirobids, and spionids (*Streblospio* spp.) were common but not abundant in the mature high marsh channel. The small tellinid, *Macoma balthica*, was also relatively common in the sedge channel but not in the mature high marsh channel. Total densities were also appreciably higher (202,205 m^{-2}) in the sedge marsh channel than in the mature high marsh (38,298 m^{-2}), a density disparity which could be primarily attributed to a nine-fold higher density of polychaetes in the sedge marsh channel. While the meiofaunal component of these dendritic marsh channels has not been well documented, it would appear that in general the infaunal invertebrate assemblages in these high-elevation channels are of significantly lower diversity than they are in lower-elevation, subsidiary and mainstem channels even though the standing stock may not be significantly different.

Although considerable variability may exist between assemblages characterizing coastal and "inland" estuary complexes of Puget Sound and the Straits of Georgia and Juan de Fuca, comprehensive information on channel infauna in the latter estuaries is generally lacking. Benthic organisms dominating sandy sediments of a blind channel in a Scirpus marsh in Puget Sound included the polychaete Manayunkia aestuarina (maximum mean density ∿4 x 10^5 m^{-2}), oligochaetes (∿2 x 10^5 m^{-2}), the gammarid amphipod Corophium salmonis (∿1 x 10^5 m^{-2}), the tanaid Tanais sp. (∿1 x 10^5 m^{-2}), and the bivalve Macoma balthica (∿ 2 x 10^3 m^{-2}) (J.E. Smith 1980). While these densities appear higher than those reported in the other studies, the differing sieve mesh sizes utilized in these studies preclude any direct comparisons.

5.2 MOTILE EPIFAUNA

Motile epifauna, due to their conspicuousness or commercial importance, tend to be more extensively documented than either infauna or zooplankton. All are essentially macroinvertebrates which have the ability to control their movement along the bottom. Some actually enter the water column during some periods (e.g., at night) and, as such, constitute the macroinvertebrate component of the estuary's nekton assemblages at these times.

As in the case of benthic infauna, information from the Columbia River estuary provides one of the most comprehensive pictures of motile epifauna in channel habitats of coastal estuaries (Columbia River Estuary Data Development Program 1980; Houghton et al. 1980; Fox 1981). Haertel and Osterberg (1967), Durkin (1973), and Kujala (1975) qualitatively described the riverine distribution of the crayfish Pacifastacus leniusculus, the oligohaline-euhaline distribution of immature sand shrimp, Crangon franciscorum franciscorum, the mesohaline-euhaline distribution of Dungeness crab, Cancer magister, and the euhaline distribution of adult C. franciscorum and C. nigricauda. Detailed biological baseline studies by Higley and Holton (1975) and Higley et al. (1979) in the Youngs Bay (mesohaline-polyhaline) region of the estuary documented the seasonal variation in the abundance of C. franciscorum. More detailed temporal and spatial documentation of the standing stock of C. franciscorum and C. magister has since been produced by the CREDDP studies (Houghton et al. 1980; Fox 1981).

Consolidated, these studies represent a relatively cohesive picture of the composition of the motile epifauna in the Columbia River estuary. Although sampling for P. leniusenlus has been neither effective nor extensive, subsidiary channels in the riverine and upper oligohaline regions of the estuary appear to harbor moderate densities of this crayfish; occurrences and densities in mainstem channels and channel slopes is low, however, and suggests that the principal location of these populations is in the littoral or shallow sublittoral habitats. At the marine end of the estuary, juvenile Dungeness crab and adult C. nigricauda and C. alaskaensis appear to be limited to euhaline water masses in the channels, although Dungeness crab were reported within the lower (seaward) polyhaline region during summer low-flow periods. Few mature or gravid Dungeness crab are found within the estuary, suggesting that these motile macroinvertebrates are moving into the estuary from spawning populations located outside the mouth of the estuary. Crangon franciscorum represents the truly endemic estuarine macroinvertebrate, particularly during the early stanzas of its life history. Adult sand shrimp appear to reproduce in the euhaline regions during winter and depart the estuary by mid-spring. Juvenile sand shrimp remain and rear within the estuary, predominantly in mudflat, sandflat and slope habitats but also in channels. The distribution of these populations gradually expands up the estuary with the intrusion of meso- and polyhaline waters during low freshwater flow through the summer months. Similar distributions and life history patterns of Crangon have been described for other coastal estuaries in Oregon (Krygier and Horton 1975).

In 1979 the mean total density and standing crop of the motile epifaunal assemblage in the channels of the Columbia River estuary ranged between 0.03 and 0.26 individuals m^{-2} and 0.03 and 1.21 g m^{-2}, respectively.

Earlier quantitative investigations of Dungeness crab in Humboldt Bay (Gotshall 1978) indicated that densities of crab in that large coastal estuary are significantly higher than in the Columbia River or Grays Harbor, which may be related to the more euhaline-polyhaline conditions in an estuary with such low riverine outflow. Demersal trawl catches indicated maxima as high as 0.5 m^{-2} in winter, 73% of which were 0+ year age recruits; the annual mean average crab density from trawl catches was estimated at 0.09 m^{-2} (actual density estimates by Armstrong et al. 1982). Underwater SCUBA surveys, however, indicated that crabs were actually more dense, averaging 0.11 m^{-2}, in August and September. Given the behavior of Dungeness crabs to burrow into sediment (MacKay 1942), seasonal and short-term variability in density estimates based upon net catches may be attributable to the various factors influencing the proportion of the population which is buried (i.e., mating, spawning, feeding, exposure during low tides, low salinities).

Extensive investigations of Dungeness crab and crangonid shrimp in Grays Harbor have been recently completed (Armstrong et al. 1982) and provide the most detailed information available on crab and shrimp abundances, movements, population dynamics and food web relationships in estuarine channel habitats. Megalops larvae of Dungeness crab appeared to have entered Grays Harbor from oceanic habitats in spring and began to metamorphose and settle in benthic habitats in the outer (euhaline-polyhaline) regions of the estuary. Juvenile crabs of the 0+ year age group (recruits) were concentrated in mudflat and adjacent channel habitats. The 1+ year age group was more abundant and distributed throughout the estuary. The 2+ year age group were less abundant than the 1+ year age group but more abundant than the 0+ year age group and were distributed predominantly in the outer region of the estuary. The 3+ year-old crabs were relatively rare and occurred only at stations close to the mouth of the estuary. Mean crab density ranged from 0.076 crabs m^{-2} to 0.012 m^{-2} and generally decreased with increasing distance up (upriver) the estuary in response to decreasing bottom salinity. Densities in the outer estuary (0.051 m^{-2}) were significantly greater than densities in the upper region of the estuary (0.030 m^{-2}) and the same was true for the period of March-August (0.048 m^{-2}) compared to the period of September-February (0.021 m^{-2}). Considerable movement between channel and shallower habitats also occurred as a possible result of tidal inundation and dewatering of littoral habitats and as a result of diel foraging behavior. The consequence of these activity patterns was that the crabs were found relatively congregated in channel habitats during daylight low tide periods. Further concentration of crabs in channel habitats was also attributed to the effects of reduced salinities in the shallower habitats during periods of high river outflow.

Qualitative summaries of motile epifauna in other coastal estuaries (Monroe et al. 1974; Percy et al. 1974; Kreag 1979a, b, c; Ratti 1979a, b; Roye 1979; Starr 1979a, b) further indicate that Dungeness crab utilize estuarine channels to varying degrees, principally depending upon the volume and spatial extent of euhaline and polyhaline water masses in the estuary. While most estuaries appear to resemble the Columbia River estuary in the limited distribution of juvenile crabs and scarsity of adult crabs, Coos and Tillamook Bays, with their greater proportional extent of euhaline and polyhaline regions appear to maintain adult populations in the lower reaches and have juvenile crab populations distributed further up the estuary than the others. Similarly, Dungeness crab populations in the "inland" estuaries of Puget Sound and the Straits of Georgia and Juan de Fuca are endemic throughout the year, although the moved lower in the estuary's channels during spring and other high freshwater flow periods.

Three species of crangonid shrimps, Crangon franciscorum franciscorum, C. nigricauda, and C. stylirostris, were found to predominate in Grays Harbor (Armstrong et al. 1982). C. franciscorum was prevalent throughout the estuary, while C. nigricauda and C. stylirostris were common only in outer reaches of the estuary; the differential distribution of C. nigricauda and C. stylirostris was attributed to lower tolerance to low bottom salinities and some form of competition with C. franciscorum. The density distribution of C. franciscorum showed strong seasonal patterns, with peak densities as high as 5 individuals m^{-2} occurring the upper reaches of the estuary in spring through summer. Shrimp densities in the outer reaches of the estuary were significantly lower (0.3-0.9 m^{-2}) and typically illustrated earlier seasonal maxima than occurred in the upper estuary. Observed diel fluctuations in shrimp density in a littoral flat habitat in the outer estuary was interpreted as a night-time habitation of shallow habitats for the purpose of feeding and movement into channel habitats during daylight in order to decrease vulnerability to predation.

In one of the few studies including motile macroinvertebrates in channel habitats of estuaries inside the Strait of Juan de Fuca, Northcote et al. (1976) described the distribution and standing crop of Crangon franciscorum through 150 km of the lower Fraser River and its estuary. Unlike its occurrence in the coastal estuaries, however, C. franciscorum was not found beyond the polyhaline region of the estuary which is restricted to the lower 10 km of the North and Main Arms Channels.

A generalized illustration and characterization of motile epifauna common to estuarine channel habitats of the Pacific Northwest are presented in Fig. 5.2 and Table 5.2.

5.3 EPIBENTHIC ZOOPLANKTON

The least understood component of estuarine communities, particularly within channel habitats, is that of the epibenthic zooplankters which occupy the boundary zone between the bottom substrate and the water column. Increased appreciation of their role in transferring detrital carbon to higher trophic levels (Kaczynski et al. 1973; Chang and Parsons 1975; Sibert 1979; Simenstad et al. 1979a), however, has recently sponsored investigations focused upon the structure, standing stock, behavior, and food web relationships of these assemblages or component taxa.

Initially, studies of epibenthic zooplankton tended to be either specifically oriented toward prominent macrofaunal taxa such as amphipods and mysids (Chang 1975; Davis and Holton 1976; Davis 1978; Levings 1980a; Pomeroy and Levings 1980) or, if assemblage-oriented, have by virtue of the collecting apparatuses been efficient only with macrofauna (Haertel and Osterberg 1967). Consequently, documentation of epibenthic meiofauna, especially from quantitative or assemblage-oriented studies, has appeared relatively recently (Crandell 1967; Higley and Holton 1975; Kask and Sibert 1976; Sibert et al. 1977b; Simenstad et al. 1979a, 1980; Houghton et al. 1980; Sibert 1981). Of these studies, however, only the CREDDP studies in the Columbia River estuary (Houghton et al. 1980) have provided a holistic, quantitative description of epibenthic meiofauna assemblages in estuarine channel habitats. A generalized illustration and characterization of epibenthic zooplankton common to estuarine habitats

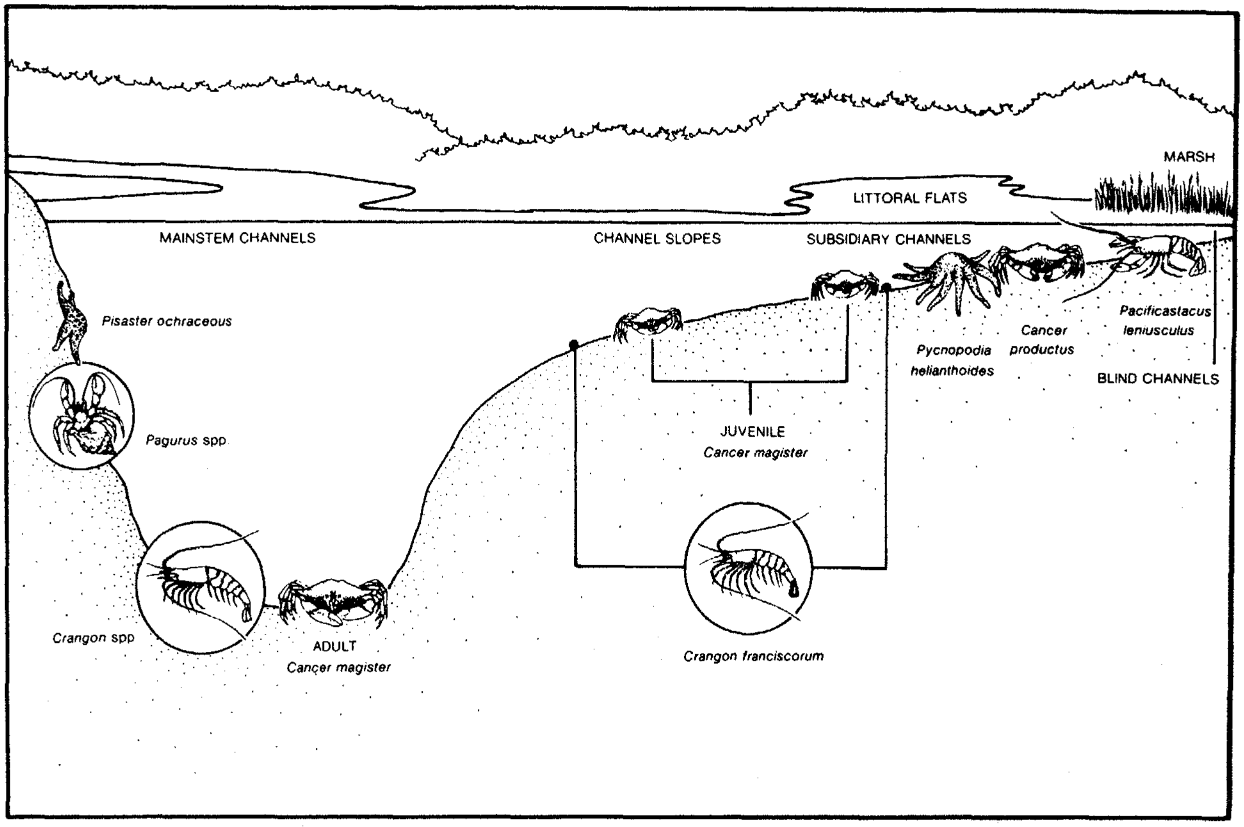

Fig. 5.2. Representative illustration of common motile epifauna assemblages of estuarine channels of the Pacific Northwest.

of the Pacific Northwest are presented in Fig. 5.3 and Table 5.3.

In conjunction with pump sampling of epibenthic zooplankton at eleven littoral and shallow sublittoral sites in the Columbia River estuary, Houghton et al. (1980) and Simenstad (Fish. Res. Inst., Univ. Wash., unpubl. data) documented the results of epibenthic sled sampling in four channel sites distributed within the estuary between April 1980 and February 1981. Over that period, epibenthic zooplankton density estimates in the channels averaged 6.7 x 10^4 organisms m^{-3} (defined as 0.5 m over the bottom) and ranged between 615 m^{-3} and 6.7 x 10^5 m^{-3}; standing crop averaged 1.02 g m^{-3} but ranged as high as 11.5 g m^{-3}. Almost two hundred separate taxonomic/life history stage categories were identified from the assemblage. The calanoid copepod *Eurytemora affinis* and undifferentiated copepod *nauplii* dominated the composition based on density, comprising 30.5% and 17.8% of the total number of organisms, respectively. There is a major question, however, whether either *Eurytemora* or copepod nauplii should be considered as epibenthic organisms since they may occur close to the bottom merely as a result of entrainment in the deeper, more saline water masses. Of the true epibenthic fauna, ectinosomatid harpacticoids (13.7%), and the cannellid harpacticoid *Scottolana canadensis* (9.5%) predominated numerically. *Eurytemora* also dominated (31.9%) the standing crop, followed by *Crangon franciscorum* (18.4%); among the true epibenthic zooplankton, *Neomysis mercedis* (6.7%), *Scottolana* canadensis (5.6%), and *Corophium salmonis* (4.6%) predominated the composition gravimetrically. Standing stock of epibenthic organisms as measured

Table 5.2. Itemization and characteristics of motile epifauna common to estuarine channel habitats of the Pacific Northwest.

Taxa	Channel Habitat[1]	Salinity Associations[2]	Sediment Associations[3]	Relevant Life History Characteristics[4]
ECHINODERMS				
Pisaster ochraceous	M	E	Cn,B	O-BC
Pycnopodia helianthoides	M	E	G,S	O-BC
DECAPODS				
Pacificastacus leniusculus	S,B	R	SC	F-ED
Crangon alaskensis	M	P-E	S,G	O-MC
C. franciscorum	M,S,B	O-E	S,G	O-MC; only juveniles extend into oligohaline
C. nigricauda	M	E	S,G	O-MC
Pagurus spp.	M		Cn,B	F-ED
Cancer magister	M,S	M-E	S,G	F-BC; Appear principally as juveniles
C. productus	M,S	M-E	SC,S	F-BC

[1] M = mainstem; S = subsidiary; B = blind.

[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline.

[3] SC = silt/clay; S = sand; G = gravel; C = cobble; B = Boulder; Cn = consolidated.

[4] O- = obligate; F- = facultative; BC = benthic carnivore; ED = epibenthic detritivore; MC = meiofauna carnivore.

by the sled in 1980 generally increased between April and May, declined in June,[3] increased again in July and August, and declined between October and February 1981. Peak mean standing stock typically occurred in the estuarine mixing (mesohaline) region of the estuary. This phenomenon could be attributed to either physical entrainment of the zooplankters within the null zone or increased production and diversity of zooplankton assemblages due to the accumulation of detrital food resources by settling and flocculation (see Section 4.2). Houghton et al. (1980) concluded that epibenthic zooplankton assemblages in the Columbia River estuary could be partitioned into the three basic assemblages described by Haertel and Osterberg (1967): 1) a riverine assemblage which is primarily a product of the freshwater Columbia River ecosystem above the estuary, 2) a euryhaline, mixing zone assemblage of indigenous estuarine species, and 3) a marine assemblage, much of which is contributed by the tidal intrusion of oceanic water through the mouth of the estuary. Some prominent taxa such as the

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[3] Sampling immediately followed the May 18 eruption of Mount St. Helens and the resulting influx of turbid freshwater into the estuary.

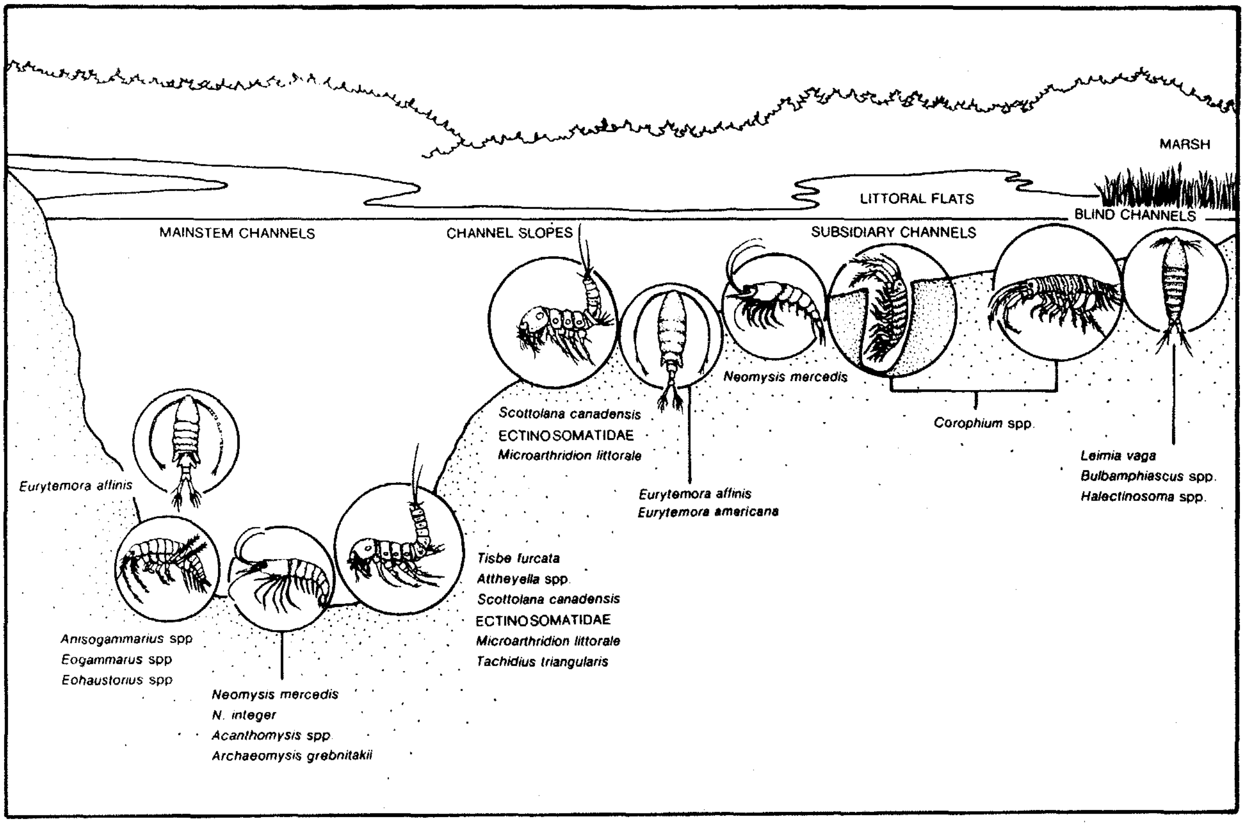

Fig. 5.3. Representative illustration of common epibenthic zooplankton assemblages of estuarine channel habitats of the Pacific Northwest.

ectinosomatids and *Scottolana canadensis*, however, are distributed ubiquitously throughout the estuary, even upstream in the riverine region.

Crandell (1967) also employed an epibenthic sled (Clark-Bumpus) and described thirty-two taxa of epibenthic harpacticoid and cyclopoid copepods in the channel habitats of Yaquina Bay, Oregon. Although the sled samples were not considered quantitative, based simply on occurrence, the prominent harpacticoid taxa included *Tisbe furcata*, *Microarthridion littorale*, *Amphiascella debilis*, *Canuella* (= *Scottolana*; Coull 1972) *canadensis*, *Parathalestris* sp. and *Schizopera* sp., and the cyclopoid copepod *Ascomyzon latum*. Crandell concluded that the epibenthic fauna in the channels during the winter were derived primarily from mudflat assemblages but that an endemic channel assemblage dominated by *Tisbe furcata* had developed by fall; this successional pattern was related to lower water temperatures in the fall and an extended period of relatively high bottom salinities which enabled more marine forms to enter the bay via the channels.

While the structure and standing stock of the channel assemblages of epibenthic zooplankton in the Columbia River and Yaquina Bay estuaries illustrated considerable temporal and spatial variation, no effort was expended to quantitatively establish the relative role of biotic (reproduction, recruitment, growth, selective predation) and abiotic (salinity, temperature, current velocities, sediment size, structure, and organic content) factors in accounting for the direction or magnitude of the variation. Williams (1983) step-wise multiple regression

Table 5.3. Itemization and characteristics of epibenthic zooplankton common to estuarine channel habitats of the Pacific Northwest.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Sediment Associations[3]	Relevant Life History Characteristics
ROTIFERA				
Brachionus spp.	M	R-0	N	
Asplanchna spp.	M	R	N	
CRUSTACEA				
CLADOCERA				
Diaphanosoma brachyurum	M	R-0	N	
Daphnia spp.	M	R-M	N	
Ilyocryptus sp.	M	R	N	
Ceriodaphnia spp.	M	R-0	N	
Bosmina sp.	M	R-0	N	
Evadne nordmanni	M	P-E	N	
Podon spp.	M	R-0	N	
Alona spp.	M	R-E	N	
Chydorus spp.	M	R-0	N	
Leydigia spp.	M	R	N	
OSTRACODA				
Limnocythere sp.	M,S	R-0	S	
COPEPODA				
CALANOIDA				
Eurytemora affinis	M,S	R-E	SC-G	
Diaptomus spp.	M	R-E	N	
Acartia spp.	M	0-E	N	
HARPACTICOIDA				
Scottolana canadensis	M,S	R-E	S	
Ectinosomatidae	M,S	R-E	S	
Microarthridion littorale	M,S	R-E	SC-S	
Tachidius spp.	M,S	R-E	S	
Laophontidae	M	R-E	S	
Paraleptastacus sp.	M	E	S	
Nitocra sp.	M	M-E	S	
Huntemannia jadensis	M	0-E	S	
Bryocamptus sp.	M	-E	S	
Attheyella sp.	M	R-P	S	
Tisbe spp.	M,S	M-E	S-G	
Leimia vaga	S,B	P-E	SC	
Bulbamphiascus sp.	S,B	P-E	SC	
Halectinosoma sp.	M-B	0-E	SC-S	
Harpacticus spp.	S	M-E	S	
Parastenhelia hornelli	S	M-E	S	
Heterolaophonte spp.	M,S	M-E	S	
Dactylopodia spp.	M,S	M-E	S	

(continued)

Table 5.3. Concluded.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Sediment Associations[3]	Relevant Life History Characteristics
CYCLOPOIDA				
Corycaeus spp.	M	R-E	N	
Cyclops spp.	M	R-E	N	
Oithona spp.	M	M-E	N	
Cyclopina spp.	M,S	P-E	Sc	
MYSIDACEA				
Acanthomysis spp.	M-S	P-E	SC-G	
Neomysis mercedis	M-S	R-E	SC-G	
N. integer	M-S	P-E	SC-G	
Archaeomysis grebnitakii	M-S	P-E	SC-G	
Holmsiella anomala	S	P-E	SC	
CUMACEA				
Lamprops spp.	S	P-E	SC	
Leucon sp.	M-S	E	S	
Leptostylis pacifica	S			
Cumella vulgaris	S-B	P-E	SC-S	
AMPHIPODA				
Corophium salmonis	M-B	O-P	SC-S	
C. spinicorne	M-B	O-P	SC-S	
Anisogammarus sp.	M-B	O-P	SC-G	
Eogammarus confervicolus	M-B	O-E	SC-G	
E. oclairi	M-S	O-E	SC-G	
Eohaustorius sp.	M-S	O-E	S	
ISOPODA				
Gnorimosphaeroma oregonensis	M-B	O-E	S-B	
Munna spp.	S	E	SC-S	

[1] M = mainstem; S = subsidiary; B = blind.

[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline.

[3] SC = silt/clay; S = sand; G = gravel; C = cobble; B = boulder; Cn = consolidated; N = no definitive sediment association.

analyses of the 1980 CREDDP epibenthic organisms data, however, provided a preliminary indication that taxonomic correlations may be more important than physical factors in explaining the variation in organism densities. *Neomysis mercedis* densities were highly correlated with *Crangon franciscorum* densities; *Scottolana canadensis* with ectinosomatid harpacticoid, *Eurytemora affinis*, and *Cyclops* spp. densities; and *Cyclops* spp. highly significantly correlated with *Crangon franciscorum*, *Neomysis mercedis*, and *Scottolana canadensis*. Physical factors, on the other hand, provided only weak correlations, i.e., *Cyclops* spp. with tidal elevation and salinity, *Scottolana canadensis* with tidal elevation and surface water temperature, and ectinosomatid harpacticoids with tidal elevation and date. Thus, while physical factors such as salinity apparently influence the distribution of epibenthic zooplankton taxa through the estuary, the standing stock structure of the various assemblages may be more the result of the distribution of food resources, theoretically detritus, and carnivores on meiofauna.

Studies of epibenthic zooplankton in estuaries within the Straits of Juan de Fuca and Georgia and Puget Sound have generally focused more upon their functional role, particularly as prey of juvenile salmonids, than upon community structure within the estuaries. Northcote et al. (1976) sampled epibenthic macroinvertebrates (>1 mm) in shallow sublittoral, slope, and channel habitats along 150 km of the Fraser River estuary and lower river. Maximum density ($\sim$100 m^{-2}) and standing crop ($\sim$500 mg m^{-2}) occurred in the North and Main Arms regions of the estuary. In most cases, comparisons of density and standing crop in the three depth habitats illustrated sharp decreases with increasing depth. Average taxa diversity tended to increase upriver and to be lowest at depths over 6 m. Dominant epibenthic zooplankton taxa included mysids (*Neomysis mercedis*, *Acanthomysis* spp.); dipteran and other insect larvae; and amphipods (*Eogammarus confervicolus*, *Corophium* spp.). Euryhaline species such as *N. mercedis* and *E. confervicolus* extended 40 km up the estuary while dipteran and other insect larvae decreased markedly between the lower mainstem and estuarine stations. Benthic oligochaetes and motile epifauna (*Crangon franciscorum*; see Section 5.2) were also dominant components of these epibenthic samples.

The distribution, abundance, and behavior of epibenthic isopods (*Gnorimosphaeroma oregonensis*) and amphipods (*Corophium spinicorne*, *Eogammarus* (*Anisogammarus*) *confervicolus*) were included in Levings and Chang's (1977) studies of the influence of current velocities upon the benthos of the Fraser River estuary. They documented that the abundance of epibenthic crustaceans collected in drift bag samplers appeared to be affected by current velocities, with maximum abundances occurring in side channels with lower current velocities. Associated laboratory studies of the activity patterns of *E. confervicolus* under different current velocities indicated that positive thigmotaxis, especially in daytime under no current flow, was overlapped with positive rheotaxis under current conditions such that behavioral compensation for downstream drift could occur up to 5-10 cm sec^{-1} velocities. This and data from similar studies in the Squamish estuary (Levings 1973) indicated that epibenthic amphipods were likely to be washed out of the estuary at higher current velocities.

Levings (1980b) further examined the vertical distribution and abundance of epibenthos in channel habitats of the lower Fraser River estuary and illustrated that *E. confervicolus* was more abundant in the bottom drift net and pump samples, where densities as high as 65 m^{-3} were reached.

Extensive sampling of meiofauna in a subsidiary tidal channel of the Nanaimo River estuary has been conducted as part of a joint study of the prey resources of juvenile salmon in the estuary (Kask and Sibert 1976; Sibert et al. 1977a; Sibert 1979; Sibert 1981). While the earliest study involved benthic core sampling of the meiofauna, later studies specifically attempted to sample only epibenthic forms more representative of the prey assemblage available to foraging fish, either utilizing an epibenthic sled (Sibert et al. 1977a) or pump (Sibert 1981). Using a diver-operated sled, Sibert et al. (1977a) described average epibenthic harpacticoid copepod densities of 9,240 m^{-3} which, although quite substantial, were still often orders of magnitude less than densities measured by comparable core samples. Structure of the sled-captured harpacticoid assemblage was numerically dominated by ectinosomids, *Tachidius discipes*, *Parastenhelia hornelli*, and *Huntemannia jadensis*; *Harpacticus* sp., *Tisbe* sp. and *Heterolaophonte littoralis* also occurred frequently in the sled samples but were not well represented in the core samples, suggesting that these are true epibenthic forms.

Further definition of the structure and diel fluctuations of epibenthic zooplankton was accomplished using an epibenthic pump with intakes located within 5 cm and 30 cm of the sediment surface. These experiments illustrated that, despite homogeneous water characteristics, significantly (2x to 20x) and persistently higher densities occurred 5 cm from the bottom than 30 cm above it. Harpacticoid (i.e., Harpacticus septentrionalis (= H. uniremis), Microarthridion littorale, ectinosomids, Dactylopodia crassipes, Tisbe spp.), calanoid (Eurytemora hirundoides), and cyclopoid copepods (Oithona sp.) formed the major taxa in the assemblage. Harpacticoids averaged between 32 and 330 m^{-3} in the higher depth strata and 370 to 2,800 m^{-3} in the lower strata. Thus, these epibenthic or "hyperbenthic" (Beyer 1958; Hesthagen 1973) assemblages could originate from both upward movement of surface-dwelling benthic species (Bell and Sherman 1980) and downward movement of planktonic species. Although the comparable roles of active migration and passive diffusion are unknown, Sibert (1981) suggested that hyperbenthic populations originate from both sinking plankton and scoured meiofauna which are physically entrained in the turbulent boundary layer. It was also suggested that such entrainment may be advantageous to the hyperbenthic organisms from the standpoint of higher concentrations of food particles trapped within the turbulent layer. Given the physical parameters determining the conditions promoting equilibrium between sinking and turbulent mixing (frictional drag velocity, particle diffusion coefficient, and current velocity), the spatial dimensions of hyperbenthic populations within various estuarine habitats and the temporal pattern of turbulent layer formation and persistence over tidal cycles are likely to be highly variable. Unfortunately, such detailed data and analyses are not available.

While considerable sampling of epibenthic zooplankton has been conducted within the Strait of Juan de Fuca and Puget Sound (Simenstad et al. 1979b; Simenstad et al. 1980), very little has occurred in estuarine channel habitats. Blaylock and Houghton (1981) utilized the same epibenthic plankton pump used in the CREDDP studies on the Columbia River estuary (Houghton et al. 1980) to sample epibenthic assemblages in Commencement Bay. Although cluster analysis of the combined littoral and sublittoral, estuarine and marine samples did not illustrate distinct epibenthic zooplankton assemblages associated with estuarine channel sites, the epibenthic assemblages in the blind (waterway) channels tended to be less diverse than the more marine or the mid-littoral sites. While the harpacticoid copepod assemblages were not described taxonomically by site, qualitative assessment of the samples has indicated that Tisbe spp., Typhlamphiascus pectinifer, and Rhynchothalestris helgolandica sp. were dominant taxa in the silty sand, epibenthic habitats of the channels (J. Cordell, Univ. Washington, personal communication). Corophium spp. was the only prevalent gammarid amphipod; Microcalanus sp. and Paracalanus sp. were prominent calanoid copepods; Corycaeus spp. and Cyclopina sp. were the most common cyclopoid copepods; and Cumella vulgaris was the dominant cumacean in the channel assemblages.

Simenstad and Cordell (1980) also described the composition and density of epibenthic organisms collected at the end of a blind channel (City Waterway) in Commencement Bay with the epibenthic sled described by Sibert et al. (1977a). Among the true epibenthic zooplankters captured by the sled (as the sled skimmed the surface sediments, the majority of the organisms captured were benthic nematodes and polychaete annelids), a low diversity assemblage of harpacticoid copepods was prominent. Bulbamphiascus sp. and Mesochcra lilljeborgi constituted the dominant harpacticoid copepods and Tisbe sp. was abundant at several sites. Overall density of epibenthic organisms within 10 cm of the bottom was estimated to average 42,020 m^{-3} and standing crop 1.1 g m^{-3}.

Although these diverse studies of epibenthic zooplankton were neither systematic nor synoptic with regard to estuarine habitats, it is evident that much variation in structure and standing crop within estuarine channel habitats exists. In cases such as blind, fine sediment channels with organic enrichment, there is evidence for dramatically different assemblages from more euryhaline, coarser sediment channels.

5.4 PELAGIC ZOOPLANKTON AND NEUSTON

Pelagic estuarine zooplankton and neuston originate from three general sources (Cronin et al. 1962; Haertel and Osterberg 1967): 1) those associated with freshwater water masses, 2) those associated with oceanic water masses, and 3) those endemic to the estuary and associated with euryhaline waters. Neustonic organisms, although constituting less well-established assemblages in estuaries as compared to freshwater or fjord habitats, where turbulence and mixing are not as extreme, may include both distinct populations of zooplankters as well as terrestrial drift organisms transported into the estuary.

Freshwater zooplankters transported into the upper reaches of estuaries can often constitute a significant proportion of the estuary's zooplankton assemblage, especially in the large coastal estuaries where the riverine systems are large enough to maintain stable zooplankton populations within the river itself. This is particularly true for the Columbia River estuary and Grays Harbor, where high densities of the cladocerans *Daphnia* spp., *Bosmina* spp., *Ceriodaphnia quadrangula*, *Diaphanosoma brachyurum*, the calanoid copepod *Diaptomus* spp., and the cyclopoid copepods *Cyclops* spp., especially *C. vernalis*, are commonly found during summer months (Haertel and Osterberg 1967; Simenstad and Eggers 1981). Haertel and Osterberg (1967) recorded the highest density (2,700 m^{-3}) of freshwater zooplankters 37 km from the mouth of the Columbia River estuary during the period of maximum temperature and lowest turbidity. The density there fell to below 100 m^{-3} during the winter period of low temperatures and high turbidity. Densities of pelagic zooplankton, including many freshwater forms, in a riverine channel habitat of Grays Harbor reached maxima of only 30-60 m^{-3} through the summer months (Simenstad and Eggers 1981).

Oceanic zooplankton inundate estuaries via the tidal intrusion of marine water masses and become most prominent during periods of lowest riverine discharge. Along the Pacific Northwest coast the prominent marine zooplankters transported into coastal estuaries include the cladocerans *Evadne nordmanni* and *Podon* spp., the calanoid copepods *Calanus* spp., *Pseudocalanus minutus*, *Centropages abdominalis*, *Epilabidocera amphitrites*, and *Acartia* spp., and the cyclopoid copepods *Coryeaeus anglicus* and *Oithona similis*; *Epilabidocera* is a neustonic form. Considerable seasonal variation in dominant zooplankters transported into the estuary occurs as a result of changes in nearshore currents and nearshore marine community structure. Miller (1972) and Frolander et al. (1973) illustrated that northern coastal or subarctic ocean species, such as the marine calanoid copepods *Acartia clausi* and *Pseudocalanus* sp., dominated the zooplankton assemblage of Yaquina Bay in summer, reflecting southerly surface currents offshore, while during the winter neritic species characteristic of the California coastal assemblages such as *Paracalanus parvus*, *Ctenocalanus vanus*, *Clausocalanus arcuicornis*, and the cyclopoid copepod *Corycaeus anglicus* were transported into the bay from northward-flowing nearshore currents and became codominant with *A. clausi*.

Prevalent marine zooplankters in Grays Harbor also varied over the spring-fall period as documented by Simenstad and Eggers (1981). *Evadne nordmanni*, *Podon* sp., *Pseudocalanus* spp., *Acartia longiremis* and *A. tonsa* were common only during summer through mid-fall; *Calanus* sp. and *Metridia lucens* occurred predominantly in late winter to early spring; and *Centropages abdominalis* and *Acartia clausi* occurred abundantly from spring through early summer. Densities of the marine zooplankton assemblage in the Columbia River estuary appeared to peak at $\sim$750 m^{-3} in the fall, with average densities of $\sim$500 m^{-3} throughout the year (Haertel and Osterberg 1967). Densities of neritic zooplankton at the entrance to Grays Harbor, which was dominated wholely by marine euhaline forms, reached an early maximum of $\sim$850 m^{-3} in April and a second, fall maxima of $\sim$200 m^{-3} but averaged <200 m^{-3} over the entire period. Mean standing crop illustrated greater fluctuations; estimates in the spring fell between 200 mg m^{-3} in April and 1 g m^{-3} in early June but reached a maximum of only $\sim$10 mg m^{-3} in the fall. The average mean standing crop over the entire period was 55 mg m^{-3}.

Endemic zooplankton which sustain populations within Pacific Northwest estuarine channels are dominated by the calanoid Eurytemora spp.; E. affinis predominates in the Columbia River estuary (Haertel and Osterberg 1967; English et al. 1980) while E. americana appears to prevail in many of the other coastal estuaries such as Grays Harbor (Simenstad and Eggers 1981), Yaquina Bay (Frolander et al. 1973), and the Salmon River estuary (Johnson 1981). Eurytemora tends to completely dominate the zooplankton assemblages in the mesohaline regions of these estuaries and can attain high population standing stock levels under certain low riverine discharge salinity regimes. Haertel and Osterberg (1967) reported two peaks in Eurytemora density in the Columbia River estuary, one in April (108 x 10^{3} m^{-3}) and another in July (39 x 10^{3} m^{-3}). Eurytemora were most prevalent when surface salinities were 0.2-8$^{\circ}/_{\circ\circ}$, when the mean of the top and bottom salinities was 0.2-16$^{\circ}/_{\circ\circ}$, and when the bottom salinity was greater than 0.2$^{\circ}/_{\circ\circ}$. Eurytemora in Grays Harbor was second (20% of mean total density) only to Acartia clausi (22%) and also illustrated two density maxima, one in late April (408 m^{-3}) and another from August to the end of October ($\sim$80 m^{-3}). In Yaquina Bay, Johnson (1981) documented that, unlike Acartia clausi which occurs seasonally in the lower reaches, the congeneric A. californiensis was able to persist as an endemic population in the upper region of that estuary.

Maintenance of endemic zooplankton populations in Pacific Northwest estuarine channels can pose a major problem due to the typically short flushing times, high degree of turbulent mixing, and net seaward flow common at almost all depths during the spring and summer. Unlike the indigenous estuarine zooplankton populations in other regions, which have evolved reproductive rates and vertical migration to compensate for the seaward loss of zooplankters, Eurytemora populations in Pacific Northwest coastal estuaries appear to be more vulnerable to depletion during high discharge flushing. Possible alternative mechanisms, such as lateral migration or entrainment in low velocity water masses such as in the null zone or epibenthic boundary layer, may explain the persistence of Eurytemora populations in these systems. Nevertheless, extreme riverine discharge and flooding have been reported to reduce Eurytemora populations in the Columbia River by three orders of magnitude (Haertel and Osterberg 1967).

A classic study of estuarine maintenance in a pelagic zooplankton population is Johnson's (1981) revealing analysis of Acartia californiensis in Yaquina Bay. The persistent occurrence of well-defined cohorts in the upper region of the estuary was concluded to result from short life expectancy of adult females, with minor reinforcement from spring tides. Assuming passive behavior, tidal flushing was estimated to remove a maximum of 3.4% to 8.7% per day, but actual behavioral utilization of the landward flowing countercurrent and residence in the estuary's null zone minimized tidal flushing losses. The abundance of adults was, however, controlled by intense, size-selective predation by zooplanktivorous pelagic schooling fishes (see Section 9.1).

In addition to normal sexual reproduction of overwintering adults, replenishment of endemic zooplankton populations after low abundances during unfavorable winter and spring months may also be enhanced by the hatching of dormant or resting eggs which have overwintered in bottom sediments, as has been documented for Acartia californiensis in Yaquina Bay (Johnson 1981).

A generalized illustration and characterization of pelagic zooplankton and neuston common to estuarine habitats of the Pacific Northwest are presented in Fig. 5.4 and Table 5.4.

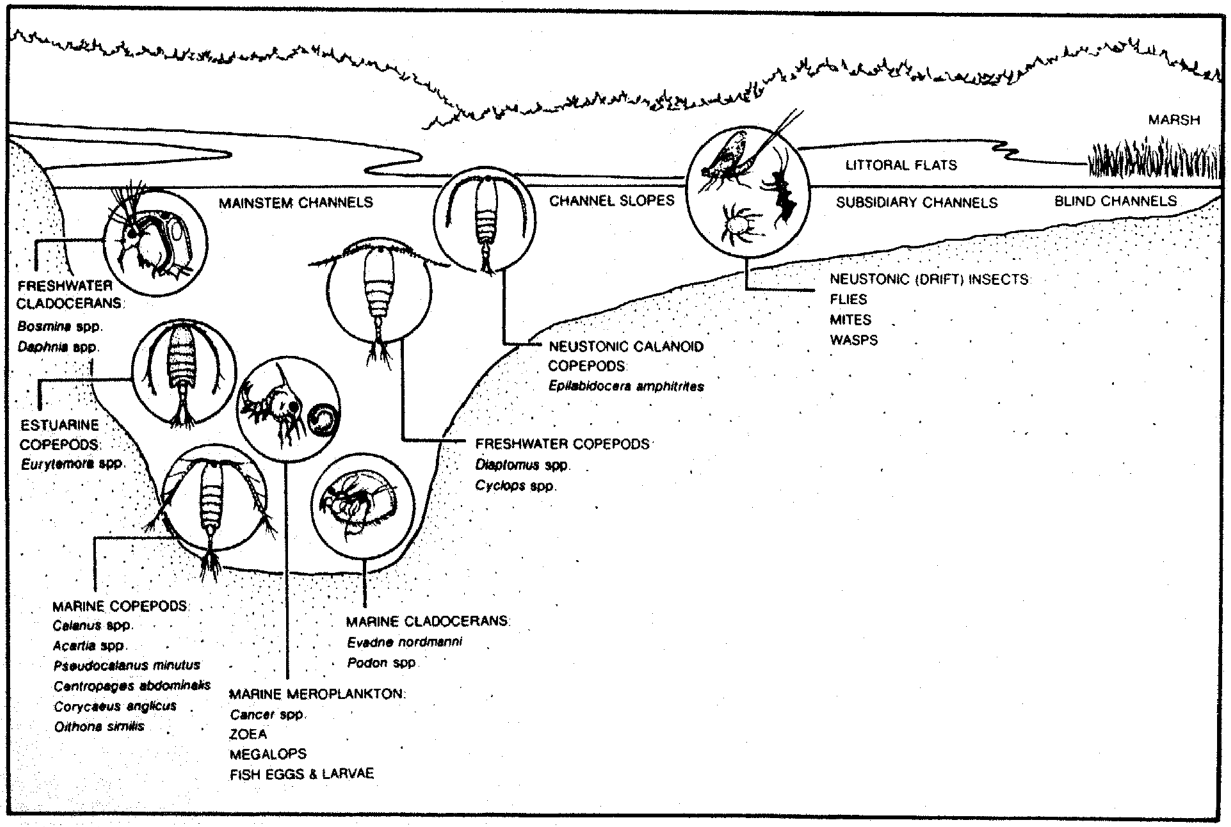

Fig. 5.4. Representative illustration of common pelagic zooplankton and neuston assemblages of estuarine channels of the Pacific Northwest.

Table 5.4. Itemization and characteristics of pelagic zooplankton and neuston common to estuarine channel habitats of the Pacific Northwest.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Relevant Life History Characteristics
COELENTERATA			
Cordylophora sp.	M	E,P	Larvae
Aeguoria sp.	M	E,P	
Aurelia sp.	M	E,P	
POLYCHAETA	M,S		
Polynoidae	M,S	E-0	Larvae
Spionidae	M,S	E-0	Larvae
GASTROPODA			
Mytilus sp.	M	E-M	Larvae and unsettled juvenile
VENEROIDA	M,S	E-M	Larvae and unsettled juvenile
Macoma sp.	M-B	E-M	Larvae and unsettled juvenile
ROTIFERA			
Brachionus spp.	M,S	R-M	
Asplanchna spp.	M,S	R-M	
CLADOCERA			
Daphnia spp.	M,S	R-0	
Ceriodaphnia quadrangula	M,S	R-0	
Bosmina spp.	M,S	R-0	
Evadne nordmanni	M,S	E-M	
Podon spp.	M,S	E-M	
Alona spp.	M,S	R-0	
Chydorus spp.	M,S	R-0	
Diaphanosoma brachyurum	M,S	R-0	
COPEPODA			
CALANOIDA			
Calanus spp.	M	E-M	
Paracalanus spp.	M	E-M	
Pseudocalanus minutus	M	E-M	
Metridia lucens	M	E-M	
Centropages abdominalis	M,S	E-0	
Diaptomus spp.	M,S	R-0	
Eurytemora spp.	M-B	R-E	
Epilabidocera amphitrites	M,S	E-0	
Acartia spp.	M	E-M	

(continued)

Table 5.4. Continued.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Relevant Life History Characteristics
HARPATCICOIDA			
Scottolana canadensis	M-B	R-E	
Huntemmania jadensis	M,S	O-P	
Bryocamptus sp.	M,S	O-P	
THALESTRIDAE	M,S	E-O	
CYCLOPOIDA			
Corycaeus anglicus	M	E-O	
Cyclops spp.	M,S	R-P	
Paracyclops fimbriatus	M,S	R-O	
Oithona similis	M	E-O	
BALANOMORPHA	M-B	E-O	Cypris larvae
MYSIDACEA			
Acanthomysis spp.	M,S	E-M	
Neomysis spp.	M-B	R-E	
CUMACEA			
Leucon spp.	M-S	E-O	
Cumella spp.	M-B	E-O	
AMPHIPODA			
Corophium spp.	M-B	R-E	Principally adult males and juveniles
Eogammarus confervicolus	M-B	R-E	Principally adult males and juveniles
Anisogammarus spp.	M,S	R-P	Juveniles
ISOPODA			
Gnorimosphaeroma oregonensis	M-B	E-O	
BOPYRIDAE	M,S	O-P	Juveniles
DECAPODA			
Crangon spp.	M,S	R-E	Principally juveniles
Cancer spp.	M	E-M	Larvae
PINNOTHERIDAE	M,S	E-O	Larvae
Upogebia pugettensis	M-B	E-M	Larvae

(continued)

Table 5.4. Concluded.

Taxa	Channel Habitats[1]	Salinity Associations[2]	Relevant Life History Characteristics
TELEOSTEI			
Engraulis mordax	M	E-M	Eggs and larvae
OSMERIDAE	M	E-0	Eggs and larvae
GADIDAE	M	E,P	Larvae
Cottus asper	M-B	R-E	Larvae
GOBIIDAE	M	E-0	Larvae
INSECTA			
EPHEMERILLIDAE	M-B	R-E	
GERRIDAE	M-B	R-E	
PLECOPTERA	M-B	R-E	
PERLODIDAE	M-B	R-E	
CHIRONOMIDAE	M-B	R-E	Including larvae
ARACHNIDA			
HYDRACARINA	M-B	R-E	

[1] M = mainstem; S = subsidiary; B = blind.

[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline.

CHAPTER 6

FISH ASSEMBLAGES OF ESTUARINE CHANNELS

According to their association with the bottom or water column, fishes of Pacific Northwest estuarine channels can be categorized respectively as demersal or pelagic. In many instances, however, there is considerable overlap in species occurrences in the two habitats due to behavioral (vertical migration, salinity preferences) or life history (demersal or pelagic larvae, spawning activity) characteristics.

6.1 DEMERSAL FISHES

Despite the typically dynamic characteristics of the benthic environs of estuarine channel habitats, diverse assemblages of demersal fish have become adapted to live and reproduce amid the turbulent mixing, high turbidities, low light levels, and variable food resources there. Unlike the salmonids, which have been studied extensively in many Pacific Northwest estuaries, demersal fish assemblages have been relatively ignored. Only recently have comprehensive research programs such as the CREDDP studies on the Columbia River estuary and those funded in Grays Harbor by the U.S. Army Corps of Engineers documented demersal fish assemblages in channels throughout the estuaries. Synthesis of these sources (Natl. Mar. Fish. Serv. 1980, 1981; Simenstad and Eggers 1981; C. Simenstad and D. Armstrong, School Fish., Univ. Wash., unpublished data) and more limited information from the Columbia River estuary (Haertel and Osterberg 1967; Durkin 1975; Durkin et al. 1976, 1979, 1981; Higley et al. 1976), other coastal Oregon estuaries (Percy et al. 1974; Reimers and Baxter 1976; Mullen 1977), the Fraser River estuary (Northcote et al. 1979), the Duwamish River estuary (Matsuda et al. 1968), and Commencement Bay (Weitcamp and Schadt 1981) indicate that 43 species (Table 6.1) of demersal fish occur commonly. Of these, nine species (denoted by *) generally occur in most estuaries (Fig. 6.1). Assemblage structure varies significantly among these estuaries, however. Sources of this variation are myriad but appear to relate principally to the relative extent of salinity intrusion, the characteristics of the freshwater watershed, geographic region, and estuarine microhabitat.

The effect of salinity intrusion and flushing characteristics in structuring the assemblage is most evident when the demersal fish assemblages of the Columbia and Fraser River estuaries are compared to those of less freshwater-dominated coastal estuaries like Coos and Yaquina Bays. Whereas euryhaline taxa such as the coastal surfperches (*Hyperprosopon* spp.) and the hexagrammids (greenlings, *Hexagrammos* spp.; lingcod, *Ophiodon elongatus*) occur commonly inside the latter bays, they seldom enter the Columbia or Fraser River estuaries beyond the narrow euryhaline region within the first 2-3 km.

The diversity of the demersal fish assemblage within a given estuary typically varies as a function of the fishes' salinity tolerances and habitat requirements. The National Marine Fisheries Service (1981) described the diversity (Shannon-Weaver Index, H') of bottom trawl-captured fishes in the Columbia River estuary as reaching a maximum mean value ($H'\bar{x} = 2.4$) between 9 and 23 km upstream from the mouth of the estuary and declining rapidly when proceeding upstream to a minimum $H'\bar{x} = 0.8$) at the riverine extreme of the estuary (Fig. 6.2a). This conforms closely to the results of Haertel and Osterberg (1967), who indicated that the greatest number of species and abundances of fishes occurred consistently within the

Table 6.1. Itemization and characteristics of demersal fishes common to estuarine channels of the Pacific Northwest.

Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Sediment associations[3]	Relevant life history characteristics[4]
PETROMYZONTIDAE				
Lampetra ayresi (River lamprey)	M-S	R-E	N	P
L. tridentata (Pacific lamprey)	M-S	R-E	N	P
SQUALIDAE				
Squalus acanthias (Spiny dogfish)	M	E	N	F-EB
RAJIDAE				
Raja binoculata (Big skate)	M	E	S-G	O-EB
ACIPENSERIDAE				
Acipenser medirostris (Green sturgeon)	M	M-E	N	F-EB
A. transmontanus (White sturgeon)	M	R-E	SC-B	F-EB
SALMONIDAE				
Prosopium williamsoni (Mountain whitefish)	M	R-M	N	F-EB
CYPRINIDAE				
Cyprinus carpio (Common carp)	M-S	R-M	SC-S	O
*Mylocheilus caurinus (Peamouth)	M-S	R-M	SC-G	F-EB
Ptychocheilus oregonensis (Northern squawfish)	M-S	R-M	N	F-EB
Rhinichthys falcatus (Leopard dace)	M-S	R-M	N	O-EB
Richardonius balteatus (Reside shiner)	M-S	R-M	N	O-EB
CATOSTOMIDAE				
Catostomus macrocheilus (Largescale sucker)	M-S	R-M	N	F-EB
GADIDAE				
*Microgadus proximus (Pacific tomcod)	M	O-E	S-C	F-EP
SYNGNATHIDAE				
Syngnathus leptorhynchus (Bay pipefish)	S-B	M-E	SC-G	O-EP; Particularly associated with eelgrass and macroalgae
CENTRARCHIDAE				
Pomoxis annularis (White crappie)	M-S	R-O	N	F-EP
P. nigromaculatus (Black crappie)	M-S	R-O	N	F-EP
PERCIDAE				
Perca flavescens (Yellow perch)	M-S	R-O		O-EP

(continued)

Table 6.1. Continued.

Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Sediment associations[3]	Relevant life history characteristics[4]
EMBIOTOCIDAE				
Amphisitichus rhodoterus (Redtail surfperch)	M-S	M-E	S-C	O-EP; Particularly associated with eelgrass, macroalgae, and structures
**Cymatogaster aggregata* (Shiner perch)	M-B	O-E	SC-B	F-EP; Particularly associated with eelgrass, macroalgae, and structures
Embiotica lateralis (Striped seaperch)	M-S	P-E	G-Cn	F-EP
Hyperprosopon argenteum (Walleye surfperch)	M	P-E	N	F-EP
H. anale (Spotfin surfperch)	M	P-E	N	F-EB
H. ellipticum (Silver surfperch)	M	P-E	N	F-EB
STICHAEIDAE				
**Lumpenus sagitta* (Snake prickleback)	M-B	O-E	SC-G	F-MB; Common to eelgrass beds
PHOLIDAE				
Pholis ornata (Saddleback gunnel)	S-B	M-E	S-G	F-EP; Particularly associated with macroalgae
AMMODYTIDAE				
**Ammodytes hexapterus* (Pacific sand lance)	M-S	M-E	S-G	O-EP; Frequently buries in sand; otherwise pelagic
HEXAGRAMMIDAE				
Hexagrammos decagrammus (Kelp greenling)	M-S	M-E	G-Cn	F-EB; Particularly associated with microalgae; pelagic larvae and early juveniles
H. lagocephalus (Rock greenling)	M	M-E	C-Cn	F-EB; Particularly associated with microalgae; pelagic larvae and early juveniles
Ophiodon elongatus (Lingcod)	M	M-E	G-Cn	O-EB; Particularly associated with microalgae; pelagic larvae and early juveniles
COTTIDAE				
**Cottus asper* (Prickly sculpin)	M-B	R-M	SC-G	F-EB
Enophrys bison (Buffalo sculpin)	M-B	E	S-C	O
**Leptocottus armatus* (Pacific staghorn sculpin)	M-B	R-E	SC-C	F-EB
Scorpaenichthys marmoratus (Cabezon)	M	P-E	S-C	O-EB
AGNOIDAE				
Stellerina xyosterna (Pricklebreast poacher)	M	P-E	S-C	F-EB
CYCLOPTERIDAE				
Liparis pulchellus (Showy snailfish)	M-S	M-E	S-C	F-EP

(continued)

Table 6.1. Concluded.

Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Sediment associations[3]	Relevant life history characteristics[4]
L. rutteri (Ringtail snailfish)	M-S	P-E	S-C	F-EP
BOTHIDAE				
Citharichthys sordidus (Pacific sanddab)	M-S	M-E	S-C	F-EP; Pelagic larvae
*C. stigmaeus (Speckled sanddab)	M-S	M-E	S-C	F-EP; Pelagic larvae
PLEURONECTIDAE				
Isopsetta isolepis (Butter sole)	M-S	M-E	S-C	F-EB; Pelagic larvae
PLEURONECTIDAE - continued				
*Parophrys vetulus (English sole	M-B	M-E	SC-C	F-EP; Pelagic larvae
*Platichthys stellatus (Starry flounder)	M-B	R-E	SC-C	F-EB; Pelagic larvae
Psettichthys melanostictus (Sand sole)	M-S	M-E	S-C	F-EB; Pelagic larvae

*Species prevalent in all Pacific Northwest estuarine channels.

[1] M = mainstem; S = subsidiary; B = blind

[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline

[3] SC = silt/clay; S = sand; G = gravel; C = cobble; B = boulder; Cn = consolidated; N = no definitive sediment association.

[4] P = parasitic on other fish; F- = facultative, O- = obligate; PP = pelagic planktivore; EP = epibenthic planktivore; EB = epibenthic benthivore; MB = meiobenthic benthivore; O = omnivore.

oligohaline to mesohaline regions no matter where this mixing region was located within the estuary due to variability in river discharge. Durkin et al. (1981) also indicated that abundance of demersal fish was highest in those channel ("scour") sites within the mixing or null zone region of the estuary, while diversity declined uniformly as distance from the mouth of the estuary increased.

The compounded effects of fish emigration, immigration, and recruitment of juveniles, and of river discharge on salinity distribution within the estuary also account for seasonal shifts in diversity of demersal fish assemblages. From the same 18-month, 22-site bottom trawl sampling series cited above, the National Marine Fisheries Service (1981) also documented that peak diversity ($H'_{\bar{x}}$ = 2.2) occurred between October and December, and minimum diversity ($H'_{\bar{x}}$ = 1.2) occurred between May and July (Fig. 6.2b). The occurrence and extent of the density minimum may, however, be unrepresentative because of the unusual effects of the dramatically-increased turbidity levels during this period as a result of the May 18, 1980 eruption of Mt. St. Helens in the Columbia River watershed. Among the principal demersal fishes in the estuary, starry flounder, prickly sculpin, and Pacific staghorn sculpin illustrated few major changes in numerical availability over the 18-month period; availabilities of shiner perch, Pacific sand lance English sole, and butter sole, on the other hand, fluctuated both monthly and seasonally; snake prickleback, sand sole, and Pacific tomcod availability varied intermediately on a seasonal scale.

6.2 PELAGIC FISHES

Unlike demersal fish assemblages, pelagic fishes in estuarine channel habitats often occur sporadically because

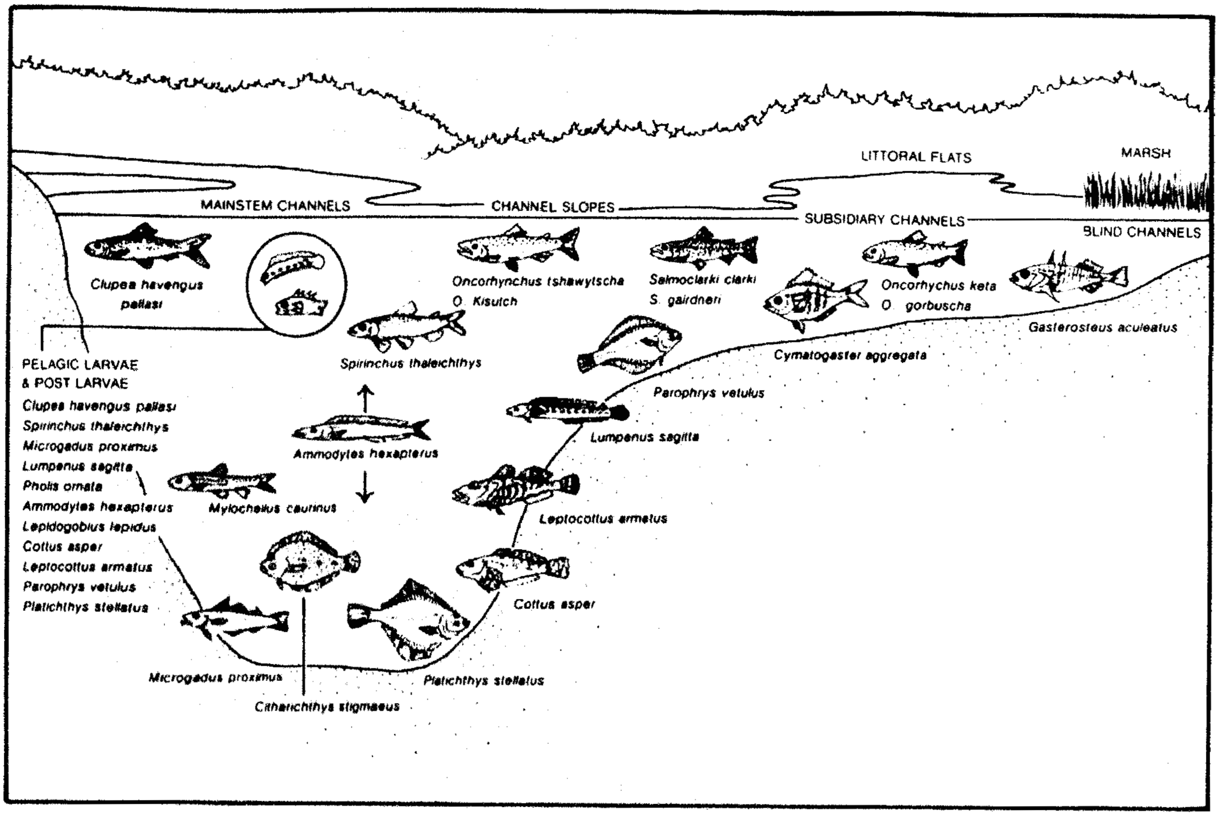

Fig. 6.1. Representative illustration of common fish assemblages of estuarine channels of the Pacific Northwest.

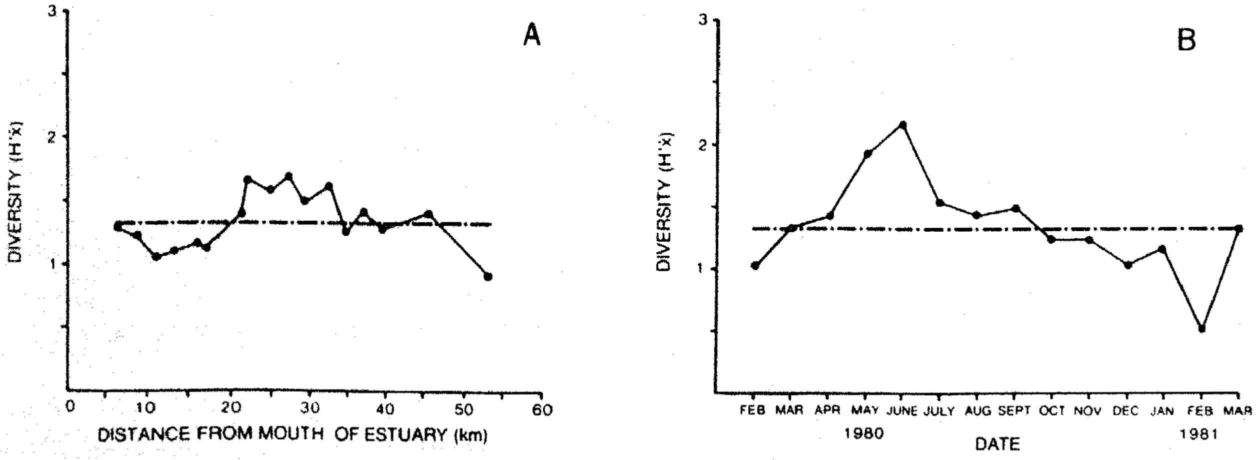

Fig. 6.2. Mean Shannon-Weaver diversity index ($H'_{\bar{x}}$) of demersal fishes in the Columbia River estuary as a function of location along the longitudinal axis of the estuary (A) and over the 18-month sampling period (B); figure from Natl. Mar. Fish. Serv. (1981).

of their motility and characteristic association with discrete water masses or as a function of life history patterns. For instance, the occurrence and residence time in the estuary of anadromous species is generally a function of migratory behavior. Many species occur solely as pelagic larvae and juveniles (meroplankton) during brief periods in their early life history but emigrate from the estuary, become demersal, or move into adjacent habitats as juveniles and adults.

Similar to the information about demersal fish, the majority of the comprehensive studies of pelagic fish assemblages in estuarine channels of the region have occurred in the larger estuaries such as the Columbia River (Haertel and Osterberg 1967; Durkin et al. 1979, 1981; National Marine Fisheries Service 1980, 1981), Grays Harbor (Simenstad and Eggers 1981), and the Fraser River (Northcote et al. 1979); some smaller, coastal estuaries have been surveyed, however, including Coos Bay (Cummings and Schwartz 1971), Tillamook Bay (Cummings and Berry 1974; Forsberg et al. 1975), the Umpqua River (Mullen 1977), and Sixes River (Reimers and Baxter 1976). Ichthyoplankton has also been addressed specifically in the Columbia River estuary (Misitano 1977; English 1980), Yaquina Bay (Pearcy and Myers 1974), and Humbolt Bay (Eldridge and Bryan 1972) and incidentally in Grays Harbor (Simenstad and Eggers 1981). Synthesis of these sources indicates that 36 taxa representing 16 families are common fishes in the pelagic assemblages of Pacific Northwest estuaries (Table 6.2). Of these, 13 are anadromous, 16 appear exclusively as ichthyoplankton, and only the remaining eight comprise taxa which could be considered to maintain extended residence in estuarine channels.

Unlike the pattern of demersal fish assemblage diversity in the Columbia River estuary, the National Marine Fisheries Service (1981) documented maximum diversity ($H'_{\bar{x}} = 1.7$) of pelagic (purse seine-caught) fishes in the central mixing region of the estuary, 20 to 35 km from the mouth, and below average diversity values in both euryhaline and riverine regions (Fig. 6.3a). Temporal diversity of the pelagic fish assemblage was also dramatically different from the demersal assemblage. In an almost mirror image of the pattern of the demersal fish assemblage, maximum diversity ($H'_{\bar{x}} = 2.2$) of pelagic fishes occurred in the spring and declined to a winter minimum ($H'_{\bar{x}} = 0.5$) in an almost mirror image of the pattern of the demersal fish assemblage (Fig. 6.3b). As noted earlier, however, the effects of increased turbidity from the eruption of Mt. St. Helens in May 1980 may bias interpretations of the May-July 1980 data.

6.2.1 Resident Pelagic Fishes

Among the common pelagic fishes in estuarine channels, the clupeids (herrings), engraulids (anchovies), osmerids (smelts), atherinids (silversides), and ammodytids (sand lances), commonly referred to as a group as "baitfish," comprise the majority of the non-anadromous, resident fishes; the three-spine stickleback comprises the only non-baitfish resident. Pacific herring utilize Pacific Northwest estuaries for spawning and rearing of larvae and early juvenile stages. Spawning typically occurs in shallow subtidal habitats between January and July, with considerable variation among estuaries. Spawning in the Columbia River estuary occurs between March and July and may involve several major spawnings (Misitano 1977; Natl. Mar. Fish. Serv. 1981). In Yaquina Bay herring spawn earlier, between January and March (Pearcy and Myers 1974), and may also undergo as many as four major spawnings (Steinfeld 1972). Accordingly, larvae may occur in the channels over a protracted period of time, between March and August in the Columbia River estuary (Misitano 1977) and between January and May in Yaquina Bay (Pearcy and Myers 1974). Spawning may be annually sporadic, however, as both English (1980) and Simenstad and Eggers (1981) reported low abundances or no herring larvae in the Columbia River estuary and Grays Harbor, respectively, in 1980. Juvenile herring, whether originating within or transported into the estuary as larvae or post-larvae, tend to

Table 6.2 Itemization and characteristics of pelagic fishes common to estuarine channels of the Pacific Northwest.

Taxa	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
CLUPEIDAE			
Alosa sapidissima (American shad)	M	O-E	O-PP; Anadromous
Clupea harengus pallasi (Pacific herring)	M	O-E	O-PP; Also occurs in ichthyoplankton; spawn in estuary
ENGRAULIDAE			
Engraulis mordax (Northern anchovy)	M	M-E	O-PP; Occur principally as larvae and juveniles
SALMONIDAE			
Oncorhynchus gorbuscha (Pink salmon)	M-B	R-E	F-PP; Anadromous
O. keta (chum salmon)	M-B	R-E	O-EP; Anadromous
O. kisutch (coho salmon)	M-B	R-E	F-EP; Anadromous
O. nerka (sockeye salmon)	M-S	R-E	O-PP; Anadromous
O. tshawytscha (Chinook salmon)	M-S	R-E	F-EP; Anadromous
Salmo clarki (cutthroat trout)	M-B	R-E	F-PPs; Anadromous
S. gairdneri (Steelhead trout)	M-B	R-E	F-PP; Anadromous
Salvelinus malma (Dolly Varden)	M-S	R-E	F-PPs; Anadromous
OSMERIDAE			
Allosmerus elongatus (Whitebait smelt)	M	M-E	O-PP; Also occurs in ichthyoplankton
Hypomesus pretiosus (Surf smelt)	M-S	M-E	F-PP; Also occurs in ichthyoplankton
Spirinchus thaleichthys (Longfin smelt)	M-S	O-E	F-EP; Anadromous; also occurs in ichthyoplankton
Thaleichthys pacificus (Eulachon)	M-S	O-E	O-PP; Anadromous; also occurs in ichthyoplankton
GADIDAE			
Microgadus proximus (Pacific tomcod)	M	M-E	O-EP; Occurs only in ichthyoplankton; demersal as juvenile and adult
ATHERINIDAE			
Atherinops affinis	M-S	O-E	O-PP; Anadromous
GASTEROSTEIDAE			
Gasterosteus aculeatus (Three-spined stickleback)	M-B	R-E	O-EP

(continued)

Table 6.2. Continued.

Taxa	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
PERCICHTHYIDAE			
Morone saxatilis (Stripped bass)	M	R-E	F-EP; Anadromous
STICHAEIDAE			
Lumpenus sagitta (Snake prickleback)	M-S	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juveniles and adults
PHOCIDAE			
Pholis ornata (Saddleback gunnel)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juveniles and adults
AMMODYTIDAE			
Ammodytes hexapterus (Pacific sand lance)	M	M-E	O-PP; Also occurs in ichthyoplankton
GOBIIDAE			
Lepidogobius lepidus (Bay goby)	M-S	M-E	O-PP; Occurs only in ichthyoplankton; moves to shallow littoral habitats as juveniles and adults
Clevelandia ios (Arrow goby)	M-S	M-E	O-PP; Occurs only in ichthyoplankton; moves to shallow littoral habitats as juveniles and adults
SCORPAENIDAE			
Sebastes melanops (Black rockfish)	M	P-E	F-PP; Also occurs in ichthyoplankton
Sebastes spp. (Rockfish)	M	M-E	O-PP; Occurs only in ichthyoplankton
HEXAGRAMMIDAE			
Hexagrammos spp. (Greenlings)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Ophiondon elongatus (Lingcod)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
COTTIDAE			
Cottus asper (Prickly sculpin)	M-B	B-P	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as junenile and adult

(continued)

Table 6.2. Concluded.

Taxa	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
Enophrys bison (Buffalo sculpin)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Leptocottus armatus (Pacific staghorn sculpin)	M-B	R-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Scorpaenichthys marmoratus (Cabezon)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
PLEURONECTIDAE			
Isopsetta isolepis (Butter sole)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Parophrys vetulus (English sole)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Platichthys stellatus (Starry flounder)	M	O-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult
Psettichthys melanostictus (Sand sole)	M	M-E	O-PP; Occurs only in ichthyoplankton; moves to demersal habitats as juvenile and adult

[1] M = mainstem; S = subsidiary; B = blind
[2] R = riverine; O = oligohaline; M = mesohaline; P = polyhaline; E = euhaline
[3] O- = obligate; F- = facultative; PP = pelagic planktivore; EP = epibenthic planktivore; PPs = pelagic piscivore

rear in estuarine waters usually > 20°/₀₀ salinity through summer and late fall. At least among the coastal estuaries, few juvenile herring continue to reside longer than 8-10 months. Although Pacific herring have been reported in inland estuaries (Fraser River, Northcote et al. 1979; Squamish River, Levy and Levings 1978; Duwamish River, Matsuda et al. 1968), most herring spawning and rearing appears to occur in the adjacent bays and fjords of Puget Sound and the Straits of Georgia and Juan de Fuca (Miller et al. 1978, 1980; Miller and Borton 1980; Trumble et al. 1977; Meyer and Adair 1978; Fresh 1979; Fresh et al. 1979; Gonyea et al. 1982). Herring spawning appears to be highly correlated with the occurrence of substrates suitable for egg deposition, such as eelgrass and macroalgae, and with moderately high water flushing rates. This may explain why herring spawning tends to be more pronounced in such coastal estuaries as Yaquina Bay and Coos Bay than in more freshwater-dominated estuaries such as the Columbia River estu-

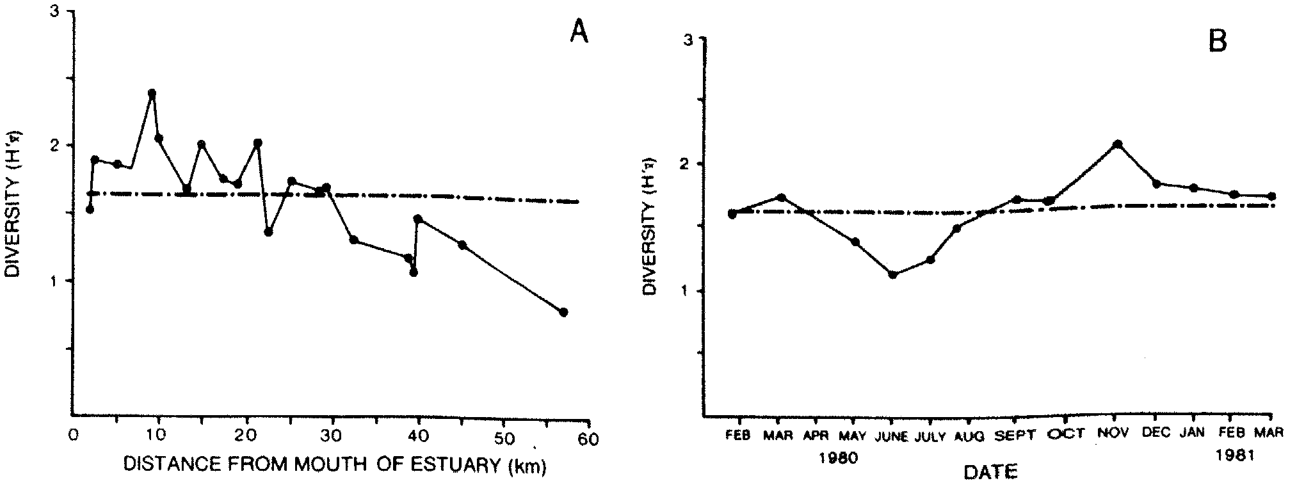

Fig. 6.3. Mean Shannon-Weaver diversity index ($H'_{\bar{x}}$) of pelagic fishes in the Columbia River estuary as a function of location along the longitudinal axis of the estuary (A) and over the 18-month sampling period (B); figure from Natl. Mar. Fish. Serv. (1981).

ary, which has no extensive eelgrass or kelp bed habitats. Rearing of larvae and juveniles in channels appears initially to be a function of offshore-estuarine circulation and later, with their recruitment from the plankton to the nekton, a function of prey (calanoid copepods, i.e. *Acartia clausii*, *Pseudocalanus* sp.) availability (Russell 1964; Pearcy and Myers 1974).

Most northern anchovy eggs, larvae, and juveniles which occur in the region's estuarine channels originate from spawning populations in adjacent coastal waters, although spawning has been reported in bays and passages of Puget Sound (Miller and Borton 1980). Richardson (1973) described concentrations of anchovy larvae in near-surface strata of the Columbia River plume between June and August and suggested that a spawning stock of anchovies was particularly associated with the plume. Eggs appear to be commonly transported into the Columbia River estuary between April and September. English (1980) described maximum densities (∿1500 m^{-2}) in June at locations nearest the mouth of the estuary. Hatching of these eggs within the estuary and further transport of larvae into the estuary account for increased concentrations of larvae and post-larvae in the euhaline to mesohaline regions over an extended period, January through November (Misitano 1977). Pearcy and Myers (1974) also collected larval anchovies (1.6×10^{-3} m^{-3}) from Yaquina Bay in July through September although densities were not as high as reported in the Columbia River estuary. Probably due to a general lack of significant sampling effort for small, schooling pelagic fishes in these estuaries, juvenile northern anchovy between post-larval and the 2+-year age classes have not been reported extensively. There is qualitative evidence, however, that they are common within estuaries (T. J. Durkin, NMFS, Hammond, OR; pers. comm.). Age 2+ and later age classes can be sampled by purse seines and are reported to occur abundantly in the lower reaches of the Columbia River estuary through much of the year (Nat. Mar. Fish. Serv. 1980, 1981; Durkin et al. 1981). Simenstad and Eggers (1981) estimated that adult anchovies maintained residence in Grays Harbor for up to 6 weeks during two periods, mid-June to early August and late August to early October, and resided longest in the region just inside the mouth of the estuary. Juvenile anchovy, on the other hand, sustained residence for a long as 11 weeks, during mid-July to early October, in the mixing zone further up the estuary.

Whitebait and surf smelts comprise the non-anadromous osmerids which utilize the region's estuaries. While spawning has not been reported in coastal estuaries, surf smelt spawn on polyhaline beaches of Puget Sound and the Straits of Georgia and Juan de Fuca (Miller and Borton 1980) and may spawn within the lower reaches of some of the more marine-influenced coastal estuaries (Quillayute River estuary, Chitwood 1981). Whitebait smelt are rare inside the Strait of Juan de Fuca, which is at the northern limit of their geographic range (Hart 1973), and little is known about their spawning behavior other than that they are presumed to spawn in coastal waters (Hart 1973). Osmerid eggs are common through much of the Columbia River estuary during April and May (English 1980) and the larvae are probably present until January (Misitano 1977); they were not reported, however, during Pearcy and Myers' (1974) extensive survey of Yaquina Bay ichthyoplankton. Both smelts are present as juveniles in the Columbia River estuary through most of the year and have been reported in relatively high densities during several months, i.e., June-July in the case of surf smelt and July-August for the whitebait smelt (Natl. Mar. Fish. Serv. 1981).

Topsmelt is the least common of these nonanadromous pelagic fishes and occurs exclusively in coastal estuaries south of the Columbia River where spawning populations are reported in Coos Bay (Schultz 1933) and the Umpqua River estuary (Mullen 1977) between late May to early July. In both estuaries topsmelt capture continued in the upper reaches of the estuary from late August through September and may have included as many as three age classes (if 0-age class fish are presumed to remain within the estuary after hatching) residing in the estuary (Schultz 1933).

Pacific sand lance are a schooling, pelagic fish which is often associated with the bottom in sandy habitats (see Section 6.1) where they periodically bury themselves (Hart 1973), a behavior related to photoperiod, food availability, and hunger (Kuhlman and Karst 1967; Winslade 1974a, b, c). Their attenuated body form and rapid swimming speed makes them one of the hardest species to capture, much less quantitatively assess their standing stock, and it is questionable that their utilization of Pacific Northwest estuaries has been documented adequately. Larvae has been reported in euhaline-polyhaline regions of the Columbia River estuary in March-April (Misitano 1977) and in Yaquin Bay in moderate densities (3.5×10^{-3} m^{-3}) from January through March (Pearcy and Myers 1974). The latter study illustrated that sand lance larvae were more abundant offshore and probably were transported into the estuary via tidal exchange. In the case of the Columbia River estuary, sand lance were captured throughout the year and were periodically abundant (Nat. Mar. Fish. Serv. 1981). Larval sand lance have been collected in the mesohaline region of Grays Harbor, and common, abundant occurrences of juveniles have occurred in polyhaline regions of the outer estuary (Simenstad and Eggers 1981).

Threespine sticklebacks are ubiquitous fish which have been reported from a variety of freshwater and marine habitats (Hart 1973; Wydoski and Whitney 1979). They inhabit a variety of estuarine habitats and are common in the surface waters of blind, subsidiary, and mainstem channels but are also found among littoral macrophytes. Reproduction occurs in both freshwater and marine habitats (Hart 1973), although Vrat (1949) has questioned the effectiveness of reproduction in saline environments. Most of the comprehensive studies in the region's estuaries illustrate consistent occurrences, abundances, and spatial distributions throughout most of the year (Mullen 1977; Northcote et al. 1979; Natl. Mar. Fish. Serv. 1980, 1981; Simenstad and Eggers 1981), although a few, typically those of inland estuaries, report fewer and less consistent occurrences (Matsuda et al. 1968; Levy and Levings 1978).

6.2.2 Anadromous Pelagic Fishes

Among the anadromous pelagic fishes

utilizing estuarine channels, over half are salmonids (Table 6.2). Because of their commercial and recreational importance, Pacific salmon and anadromous trout have long been the focus of intensive studies in estuaries throughout the region both as juveniles migrating from freshwater to rear in marine habitats and as adults returning to spawning rivers. Although there is no comprehensive synthesis of this mass of knowledge, Iwamoto and Salo (in prep.), Durkin (1982), Healey (1982), Myers and Horton (1982), and Simenstad et al. (1982b) have included much of the existing information on estuarine utilization by salmon and further references can be secured from Levy (1980b) and Columbia River Estuary Data Development Program (1980). While there has been no comparable syntheses of the ecology of anadromous trouts in this region, Royal (1972) provides the most comprehensive discussion to date.

Anadromous trouts--cutthroat, steelhead, and Dolly Varden--are comparatively less abundant than the salmon and appear to utilize estuarine habitats sparingly; estuarine channels act principally as corridors for their seasonal migrations betwen freshwater spawning habitats and marine feeding habitats. After 2 to 9 years (typically 3 years) in freshwater, coastal cutthroat initially immigrate to estuarine and marine habitats during the spring and reside there until late summer and fall (Wydoski and Whitney 1979). Of all the trouts, cutthroat trout and Dolly Varden may utilize estuarine channels the most, since throughout their marine period they appear to stay in the vicinity of their home streams and often reside permanently within estuaries (Levy and Levings 1978). Although sustained estuarine residence has seldom been illustrated, Giger (1972) indicated that pre-smolt cutthroat (up to 170 mm FL[4]) which moved into the Alsea River estuary in the later part of the spring emigration maintained nonmigratory residence within the estuary. Both steelhead and Dolly Varden immigrate through the estuary from freshwater to the ocean in late winter and spring, although the racial population structure of steelhead is such that some juvenile steelhead may be found migrating to sea during every month of the year (Wydoski and Whitney 1979). Similarly, while Dolly Varden appear to be limited to subsequent emigration back into freshwater in late summer though early fall, migrating steelhead may pass through the estuaries throughout the year. The principal periods when adult steelhead ascend spawning streams is from December to March (termed "winter run" fish) or between July and September ("summer run") (Wydoski and Whitney).

The occurrence and extent of utilization of estuarine channel habitats by five species of Pacific salmon are highly variable because of their diverse life history patterns (Table 6.3). Extended occupation of estuaries beyond the normal time required for direct migration to and from the ocean is suggested to benefit salmon by providing an environment for productive foraging, physiological transition, and refugia from predators (Simenstad et al. 1982b). Estuarine residence, the habitats occupied, and the total residence time of outmigrating juveniles are determined primarily by the timing of and size at entry into the estuary. These, in turn, are correspondingly influenced by numerous abiotic and biotic factors operating in the freshwater system, i.e., time of adult spawning, stream temperatures during and after egg incubation, fry size and condition, population density in the stream, food quality and quantity, stream discharge and turbidity, physiological change, tidal cycles, and photoperiod (Iwamoto and Salo, in prep.).

Juvenile pink and chum salmon typically enter the estuaries at 30-40 mm FL, and occupy littoral and shallow sublittoral habitats in the estuary. When they are 45-55 mm FL, they begin occupying the pelagic surface of channels until they leave the estuary. Similarly, subyearling (often referred to as "fry") chinook salmon which enter the estuary 30-50 mm FL in size also tend to occupy

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[4] FL = Fork length.

Table 6.3. Life history characteristics of five species of Pacific salmon in northeastern Pacific Ocean region (modified from Simenstad, in press).

Life History Phase	Salmon Species				
	Pink	Chum	Coho	Sockeye	Chinook
Spawning Location and Timing	Some in small tributaries and estuarine intertidal, most in large tributaries and main rivers; occurs over one to two months in early fall; primarily odd years in Pacific Northwest and Southeastern Alaska, even years elsewhere in Alaska	Some in small tributaries and estuarine intertidal, most in large tributaries and main rivers; occurs over one month from early fall through early winter	Primarily in small rivers and tributaries and side channels of large rivers; occurs over one to two months from late fall through early winter	Tributaries to lakes, some along lake shoreline; occurs over two to four months from late summer to late fall	Some in tributaries, most in main rivers; occurs over one to two months in fall except for "spring chinook" populations, which spawn over three to six months in spring through early fall; small summer runs occur in Puget Sound and the Columbia River and a winter run occurs in the Sacramento River
Duration of Egg Development	Three to five months	Three to five months	Two to five months	Three to five months	Three to five months
Timing of Fry Emergence	Mid- to late winter	Mid- to late winter, early spring	Mid-winter	Early to late winter	Mid-winter to late spring except for "spring chinook" populations, which emerge from fall through mid-winter
Freshwater Rearing Timing and Duration	Usually migrate immediately after emergence	Usually migrate immediately after emergence; one month maximum	Throughout the year, 12-28 months in stream; as long as three years in Alaska	Through one to three years in lake	Spring through summer, three to four months in stream, except for "spring chinook" populations, which tend to rear for full year in estuary
Duration and Timing of Emigration to Estuary	Occurs over one month between mid-winter to early spring	Occurs over one month between mid-winter and late spring	Occurs over one to four months in late winter to early summer	Occurs over one to two months in early to late spring	Occurs over one to two months from mid-winter to late summer except for "spring chinook" populations, which emigrate from fall through winter
Duration and Location of Residence in Estuary and Nearshore Marine Environment	Less than one week in shallow habitats, three to five weeks in neritic habitats	One to three weeks in shallow habitats, three to five weeks in neritic habitats; some extended rearing, up to six months, in inland seas	One to two months in neritic habitats; some extended rearing, up to six months, in inland seas	Short-term; one to two weeks in neritic habitats	One to three weeks in shallow habitats, two to six weeks in neritic habitats; some extended rearing, eight to ten weeks or longer, in large estuaries and inland seas
Preferred Prey Organisms in Estuary	Calanoid copepods, and larvaceans in neritic habitats	Harpacticoid copepods and gammarid amphipods in shallow sublittoral habitats; calanoid copepods, decapod larvae, and larvaceans in neritic habitats	Gammarid amphipods in shallow sublittoral habitats; decapod larvae and euphausiids in neritic habitats	Juvenile shrimp and euphausiids in neritic habitats	Gammarid amphipods, cumaceans, and emergent and drift insects in shallow sublittoral habitats; drift insects, decapod larvae and fish larvae in neritic habitats
Migration and Residence in North Pacific	Along coast in Gulf of Alaska, Eastern Bering Sea and Aleutian Islands for approximately one year	Along coast in Gulf of Alaska, Eastern Bering Sea and Aleutian Islands for three to five years	Along coast in Gulf of Alaska and Eastern Aleutian Island for one, usually two years	Along coast and in Gulf of Alaska for two to three years except for western Alaska populations, which also mature in Bering Sea and Aleutian Islands	Along coast in Gulf of Alaska, Eastern Bering Sea and Aleutian Islands for one to five, typically three years
Timing of Return Migration to Estuary/Natal Stream	Late summer to early fall	Early fall to early winter	Late summer to mid-fall	Mid-summer to early fall	Fall except for "spring chinook" populations, which return in mid-spring through early fall

littoral and shallow sublittoral habitats, particularly salt marshes, mudflats, and foreshore areas before they grow larger and move into the pelagic environs (Levy and Northcote 1981; Congleton et al. 1982). Little is known about the distribution of chinook (fry) during flood tide cycles when saltmarsh and mudflat habitats are inundated. It is often presumed that they move about and feed over the littoral flats. Healey (1980), however, captured no juvenile chinook (fry) in this habitat of the Nanaimo River estuary during purse seine sampling at flood tide and the fish were found across the landward margin of the flats along the edge of the saltmarsh. A similar distributional pattern was also documented for juvenile chum in the Nanaimo River estuary (Healey 1979). But the fish are at least periodically congregated in the blind and subsidiary channels which transect most littoral and shallow sublittoral flat habitats during ebb tide cycles, and it is here that most biological sampling has been concentrated (Fig. 6.4). Fingerling and yearling chinook and coho smolts emigrate directly into the pelagic habitats of estuarine channels and, except for occasional forays into shallow sublittoral habitats, reside within this habitat until they depart the estuary.

Almost all juvenile salmon migrate into estuarine habitats between mid-winter to late summer, with some species illustrating concentrated migration periods (pink, chum, sockeye) and others (coho, chinook) protracted migrations as a result of variable population (racial) and environmental factors. Table 6.4 (Simenstad et al. 1982b) summarizes documented species residence times (total time juvenile salmon of particular species occur in estuarine habitats) for Washington State estuaries, and illustrates that juvenile pinks may occur in some estuaries over as little as four weeks while juvenile chinook may occur over as long as 29+ weeks. In estuaries adjacent to Puget Sound and the Straits of Georgia and Juan de Fuca, where resident chinook ("blackmouth") and coho salmon populations are sustained, juvenile and immature chinook and coho may continue to frequent euhaline segments of estuarine channels sporadically throughout the year (Simenstad et al. 1982b).

Species residence times, however, reflect both the variable turnover in transitional migrants from a diverse spectra of stocks and variable periods of sustained residence of each cohort group within the estuary. Unfortunately, the extensive and expensive methodology has limited the number of reliable estimates of individual residence times and identification of the factors regulating estuarine residence. Simenstad et al. (1982b) have listed estimates of maximum residence time for chum, coho, and chinook salmon, including several specific to estuarine channel habitats, in Washington estuaries (Table 6.4). Both juvenile chum and chinook (fry) appear to have short residence times in saltmarsh tidal channels, on the order of four and six days, respectively (Congelton et al. 1982). This is further supported by Levy and Northcote's (1981) approximation of 6 days individual residence time of juvenile chinook in a Fraser River estuary blind tidal channel. However, because most of these saltmarsh/mudflat tidal channel studies examined residence in only one channel system and because occupation of a specific channel may be brief, overall residence throughout the blind and subsidiary channels of saltmarshes and tide flats may be significantly longer. Levy and Northcote (1982) indicated maximum individual residence times of 30 days for juvenile chinook (fry), 11 days for chum, and two days for pink. Levy et al. (1979) had also indicated that juvenile chinook (fry) had the strongest fidelity to particular tidal channel areas, followed by juvenile chums, and juvenile pinks. They suggested shortest residency for juvenile pink salmon, intermediate residency for juvenile chum, and longest residency for chinook (fry); the variation in residency was possibly related to their distribution within the channels and the timing of emigration on ebbing tides. Detailed multivariate analyses of spatial differences in tidal channel utilization by juvenile salmonids in Fraser River

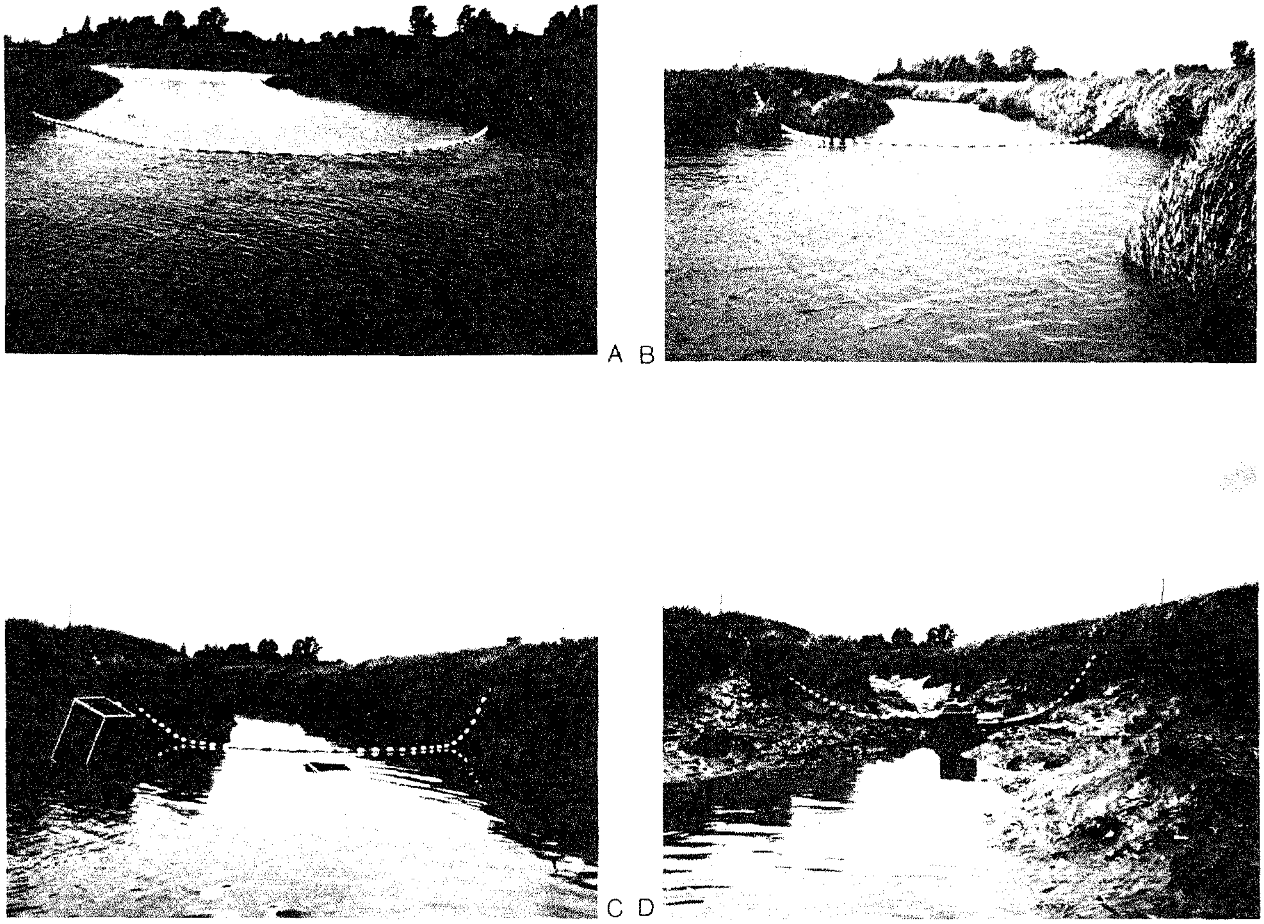

Fig. 6.4. Tidal channel trap net set in blind channel of Fraser River estuary to sample juvenile salmon utilizing saltmarsh habitat; net is set at flood slack (A), allowed to sample through the ebb tide (B, C), and sampling culminated at ebb slack (D) when only a small depth of water remains in the channel (photographs courtesy of David Levy, Westwater Research Centre, University of British Columbia, Canada).

saltmarshes has also indicated that juvenile chinook (fry) abundance is highly correlated to the amount of habitat available to the fish. Lower (bank) elevation areas tend to support higher densities of juvenile chinook (fry) (Levy and Northcote 1981). Variables included tidal channel descriptors such as mouth width, station width, channel length, channel order, sub-channel length, mean angle of channel bank, tidal slope, high tide height, tidal channel area, bank elevation, area of subtidal refugia, and number of hours of tidal channel submergence prior to sampling; (see Appendix C).

Following residence and growth in the littoral flat channels, juvenile chum and chinook (fry) move into larger subsidiary and mainstem channels (Healey 1979, 1980; Simenstad and Eggers 1981). This transition from littoral and shallow sub-

Table 6.4. Species residence times (weeks)[1] of juvenile salmon in Washington State estuaries; maximum individual residence times (days) are indicated in parentheses (from Simenstad et al. 1982b).

Estuary	Pink	Chum	Coho	Sockeye	Chinook	Source
Northern Puget Sound (nearshore)	4	6	12	12	6	Miller et al. 1978
North Sound (Bellingham Bay)		11+	11+		11+	Tyler 1964
(Bellingham Bay)		7+	7		6+, (~20)	Sjolseth 1969
(nearshore)	4	6	6		6	Miller et al. 1978; Fresh 1979
Skagit Bay/Port Susan (Kiket Island)	13	13	12		15, (50)	Stober et al. 1973b
(saltmarsh)		14+, (4)			16+, (6)	Congleton et al. 1982
Elliott Bay (lower Duwamish)		9	5		8, (42)	Bostick 1955
(estuary)					8	Salo 1969
(lower Duwamish)		12	14+		16+	Meyer et al. 1981b
Commencement Bay (estuary)	16+	8	9		9+	Puyallup Indian Nation, unpubl.
(Hylebos Waterway)		9			8+	Meyer et al. 1981a
Nisqually Reach	12	17+	15, (~40)		11+	Fresh et al. 1979
Hood Canal	18	23, (32)	15, (6)		13	Salo et al. 1980
Strait of Juan de Fuca	14	14	14		16+	Simenstad, unpubl.
Quillayute River estuary		5, (32)			18+	Chitwood 1981
Grays Harbor		10				Wendler et al. 1954
		10+, (~30)	12		29+, (~189)	Simenstad and Eggers 1981

[1] - and + indicate less than and greater than the values given, respectively.

littoral channel habitats to utilization of pelagic, mainstem channel habitats generally occurs when both juvenile chum and chinook (fry) reach 50-60 mm FL (Levy et al. 1979; Healey 1980; Levy and Northcote 1981, 1982; Reimers 1973; Simenstad and Eggers 1981). A number of mechanisms accounting for this shift in habitat utilization have been proposed, including salinity and temperature preference (Dunford 1975; Healey 1980), behavioral responses as a function of density and size (Reimers 1973; Myers and Horton 1982), and the availability of preferred prey organisms or ontogenetic changes in food habits (Simenstad and Eggers 1981; Simenstad and Salo 1982).

Individual residence times in the mainstem channels vary as a function of the period in the salmon migration, size of the fish, and density of the estuarine population. Juvenile pink salmon appear to emigrate directly out of the estuary, since no records of pelagic residence are available for Washington (Table 6.4) or other estuaries in the region. Juvenile chum may reside in pelagic habitats of mainstem channels for an additional two to four weeks (Table 6.4; Manzer 1956; Mason 1974; Healey 1979) but seldom occur in these environs when larger than 75-80 mm FL. Healey (1979) also indicated that juvenile chums from the early portion of the outmigrating population resided in the Nanaimo River estuary considerably longer than those which entered the estuary later in the outmigration. Salo et al. (1980), Simenstad and Salo (1982) and Bax (1982), however, have documented the opposite relationship in Hood Canal, where migration rates tended to be higher and residence times shorter for the earlier outmigrating population. Juvenile chinook (fry) may reside in estuarine channels longer than six months, but residence is quite variable among estuaries. Reimers (1973) identified five life history variations in the population of fall chinook in Sixes River, Oregon. The prominent type resides in the estuary a relatively short time (eight weeks) before emigrating to the ocean whereas a second type rears almost twice as long but is measurably less abundant in the estuary (17% of total migrants); the latter life history type, however, typically contributed over 90% of the returning adults. The other types passed rapidly through the estuary either as fry or as yearling smolts but were seldom abundant. Although earlier work (Simms 1970) estimated brief, i.e., 10-15 days in spring and summer and 7-10 days later in the year, residence times for juvenile chinook (fry) in the Columbia River estuary, more recent results (Natl. Mar. Fish. Serv. 1981) from on-going mark and recapture experiments have indicated extended residence from April through October. Residency patterns very similar to those documented in the Sixes River estuary have also been described for juvenile fall chinook (fry) in Grays Harbor (Simenstad and Eggers 1981), the Duwamish River estuary (Salo 1969), and the Quillayute River estuary (Chitwood 1981). Chinook smolts (yearling) probably appear in estuarine channels only transitionally, as no significant estuarine residence times have been described for this life history type. Similar to yearling chinook, coho smolts also utilize estuarine channels principally as corridors for direct emigration to the ocean (Sjolseth 1969; Simms 1970; Chitwood 1981; Natl. Mar. Fish Serv. 1981), but residence times as long as four to eight weeks have been documented (Grays Harbor, Simenstad and Eggers 1981). No information on individual residence times of sockeye smolts is available nor is there an indication that they utilize estuarine channels other than for their immediate migration from lacustrine rearing habitats to the North Pacific Ocean. In fact, the occurrence of juvenile sockeye in estuarine channels has only been documented for the Columbia River (Natl. Mar. Fish. Serv. 1980, 1981), Fraser River (Northcote et al. 1979), and the Quillayute River estuaries (Chitwood 1981).

Entry of adult salmon into estuarine channels prior to their migration upriver occurs essentially year-round, although the maximum migration period is typically between July and September (Table 6.3 and 6.5). Although timing of return is principally determined by the genetic attributes of the different species and populations, external influences such as oceanic temperature and current patterns, prey resources and photoperiod add elements of variability to the temporal distribution of returning spawners (Simenstad et al. 1982b). Once in the estuary, fish may aggregate in specific, "staging" areas before initiating the final phase of their spawning migration; upriver movements are probably stimulated by increases in river discharge, changes in water temperature and air pressure, and tidal cycles. As a result, residence time of adults within estuarine channels, although typically brief, has been estimated to range from 1-6 weeks (Simenstad et al. 1982b; Table 6.5) and the fish are often subjected to intense commercial and recreational exploitation in these channel staging areas during this period.

Other anadromous fishes include American shad, longfin smelt, eulachon, and striped bass. Of these, American shad and striped bass are distributed principally in the southern coastal estuaries of the region, although striped bass have been reported in Puget Sound (Miller and Borton 1980) and American shad occur in apparent spawning populations in several Puget Sound estuaries--Nooksack, Skagit, Stillaguamish, and Skykomish (Miller and Borton 1980). These latter two species were not originally indigenous to the west coast and have continued to expand their distribution from San Francisco Bay where both were introduced in the late 1800's or from the Columbia River where shad were introduced in 1885-1886 (Hart 1973; Wydoski and Whitney 1979).

American shad are the more prominent, especially in the large coastal estuaries such as the Columbia River and Grays Harbor. In the Columbia River the adult migration through the estuary is usually initiated in May, coincident with 13-18°C water temperatures (Leggett and Whitney 1972), and peaks in June and July. Juvenile (young-of-the-year) shad enter the

Table 6.5. General estuarine run timing and estimated individual residence times for adult Pacific salmon in Washington State estuaries (from Simenstad et al. 1982b).

Species	Run timing[1]		Estimated individual residence (time in days)		
	Peak	Range	Minimum	Maximum	Data source
Pink (only in odd years)	Late July-early Aug.	June-Sept.	6.9 8.1	13.7 32.2	Barker 1979 Barker 1979
Sockeye	July	June-Aug.	-	-	
Coho	Late Oct.	Sept.-Nov.	13.0 9.2	40.0 14.7	Eames et al. 1981; in press Barker 1979
Chinook	Late Aug.-early Sept.	July-Sept.	27.4	39.6	Stauffer 1970
Chum	Mid-Oct.-early Nov.	Sept.-Dec.	11.0 3.0 13.0	40.0 6.8 20.6	Eames et al. 1981; in press Barker 1979 Olney 1976

[1] From various Washington Department of Fisheries (Harvest Management Division) data sources.

estuary beginning in August and reside there, reaching maximum density in November and December, until emigrating to the ocean as yearlings when the young-of-the-year shad become numerous in October (Hammann 1981; Natl. Mar. Fish. Serv. 1981). Simenstad and Eggers (1981) reported a maximum sustained residence of at least 10 weeks, but their sampling did not extend beyond October.

Longfin smelt and eulachon are anadromous osmerids that migrate through Pacific Northwest estuaries as adults during winter months, but some spawning may actually occur in the more freshwater-dominated systems such as the Columbia River estuary (Misitano 1977; Natl. Mar. Fish. Serv. 1981). Up to three different age classes of longfin smelt, dominated by the young-of-the-year and yearlings, were identified in the Columbia River estuary (Natl. Mar. Fish. Serv. 1981). Residence of young-of-the-year was sustained from June through the winter of the following year but was confused by the influx of spawning adults in the fall. Occurrence of longfin smelt documented by Simenstad and Eggers (1981) indicated more ephemeral distribution of juveniles in Grays Harbor, at least in the inner reaches of the estuary, where three major influxes (the longest residence lasting 9 weeks) were evident between March and October. Juvenile longfin smelt also appear to utilize estuarine channels within Puget Sound (Duwamish, Skykomish, Stilliguamish, Skagit and Nooksack River estuaries; Miller and Borton 1980) and the Straits of Georgia (Fraser River estuary; Northcote et al. 1979), but they are much more common in the neritic habitats outside the estuaries proper (Stober et al. 1973a; Miller et al. 1978, 1980; Fresh 1979). Compared to longfin smelt, eulachon are somewhat less prominent in estuarine channels, but both adults and juveniles are common in estuaries of rivers with spawning populations, notably the Columbia River (Smith and Saalfield 1955; Haertel and Osterberg 1967; Natl. Mar. Fish. Serv. 1981), Fraser River (McHugh 1939, 1940; Northcote et al. 1979), Squamish River (Levy and Levings 1978), Nooksack River (Wydoski and Whitney 1979), and Puyallup River (Commencement Bay, Miller and Borton 1980) estuaries. Although eulachon were reported to occur in Grays Harbor (Smith et al. 1980), none were captured during the extensive sampling in that estuary described by Simenstad and Eggers (1981). Their occurrence in the Columbia River estuary is concentrated between February and May as a result of the migration of adults into the estuary and its tributaries and the downstream drift of the yolk-bearing larvae through the estuary (Misitano 1977; Natl. Mar. Fish. Serv. 1981). Despite this brief occurrence, Misitano (1977) listed eulachon as the second most abundant (19% of total) larval, post-larval, and juvenile fishes in the Columbia River estuary. Prolonged residence within the estuary appears to be minimal, however.

Although only a relatively recent addition to the anadromous fishes in the region, striped bass have become prominently established in Coos Bay (Roye 1979) and Umpqua River estuary (Mullen 1972, 1974; Ratti 1979a). Residence of adults in Coos Bay may be continuous, although some may emigrate to the ocean, and then migrate upriver to spawn between May and July. Juveniles spend the first year in riverine habitats before immigrating to the estuary.

6.2.3 Ichthyoplankton

In addition to those pelagic fishes which are found in estuarine channels throughout their development from larvae or postlarvae to at least juvenile stages, approximately 17 species also occur as prominent ichthyoplankters but move either into other microhabitats within the channels or into adjacent estuarine, marine, or riverine habitats (Table 6.2). Those which undergo ontogenetic transposition from pelagic to demersal modes within the channels include Pacific tomcod, snake prickleback, saddleback gunnel, rockfishes, greenlings and lingcod, all four species of cottids and four species of pleuronectids. Of these, prickly, Pacific staghorn, buffalo sculpins, and snake prickleback are the more common and abundant (Eldridge and Bryan 1972; Pearcy and Myers 1974; Misitano 1977; Simenstad and Eggers 1981). Among those which settle out in adjacent habitats, the bay goby is the most prevalent as an ichthyoplankter before it assumes its ultimate juvenile and adult residence in shallow sublittoral and littoral flat habitats. Bay goby larvae are especially abundant in the more southern coastal estuaries where they are as abundant as, or second in abundance to, the predominant Pacific herring larvae, but they are relatively rare in and north of the Columbia River estuary.

Occurrence of ichthyoplankton in the region's estuaries is essentially a winter-spring phenomenon, both in terms of species richness (as many as 18 species per sample) and density (maxima between 0.4 and 11.0 larvae m^{-3}) in the coastal estuaries. Tidal and diel variation can be considerable and is often associated with location in the estuary; for example, tidal excursion of water masses with particularly high densities of larvae can result in high catches during ebb tide periods (Pearcy and Myers 1974), especially in situations where shallow sublittoral and littoral flat habitats are sources of larvae. Contributions of predominantly offshore, i.e., marine, species into the more saline, lower reaches of the estuaries also promotes higher species richness in these regions. Pearcy and Myers (1974) itemized 19 taxa of fish larvae in Yaquina Bay which were characteristic of offshore assemblages, as compared to ten taxa associated with bay assemblages, and Misitano (1977) documented a steady decline in the number of species of larval, post-larval, and juvenile fishes collected at progressively more estuarine to riverine locations in the Columbia River estuary.

While many of the same assemblages and patterns that occur in the coastal estuaries may characterize inland estuaries, there is no comparable information on the ichthyoplankton in estuarine channels inside of the Strait of Juan de Fuca. Blackburn's (1973) documentation of the ichthyoplankton assemblages offshore of the Skagit River delta indicate that taxonomic similarities may exist, with the addition of several species of gadids (Pacific cod, Gadus macrocephalus, and Pacific hake, Merluccius productus) and pleuronectids (slender sole, Lyopsetta exilis), but spatial or temporal distribution and abundance of larvae within the estuary's channel habitats were not assessed.

CHAPTER 7

BIRD ASSEMBLAGES OF ESTUARINE CHANNELS

Although some of the resident and migratory bird species utilizing Pacific Northwest estuaries do not frequent channel habitats, most of these estuaries' avian fauna occupy channels at some time for foraging and roosting, and some are dependently bound to the habitat through critical food web linkages. Several species, notably the migratory waterfowl, can occur in such high abundance that they play significant, though often seasonal, roles in the food-web dynamics of these estuaries.

Adopting Peterson and Peterson's (1979) classification of littoral flat birds into ecological assemblages or "guilds,"[5] estuarine channel birds have been categorized into four assemblages primarily as a functon of their foraging behavior: 1) shallow-probing and surface-searching shorebirds; 2) waders; 3) surface and diving waterbirds; and 4) aerial-searching birds.

Habitat-specific inventories and descriptions of birds of Pacific Northwest estuaries are rare and typically inadequate in the scope and resolution of the documentation of bird distribution, abundance, behavior or ecology. Jones and Stokes Associates, Inc. (in prep.) is the most complete in terms of temporal (seasonal) and spatial (habitat, areal) documentation of birds occurring in any one estuary (e.g., the Columbia River). Other estuary-oriented accounts include Yocum and Keller (1961), Ives and Saltzman (1970), Smith and Mudd (1976a), Seaman (1977), Crawford and Edwards (1978), Peter et al. (1978), and Edwards (1979). More taxa-specific documentation includes Wetmore (1924) on grebes, Henny and Bethers (1971) and Bayer (1978) on great blue herons, Erskine (1971) on buffleheads, Couch (1964) on sandpipers, Penland (1976) on terns, and Vermeer and Levings (1977) on ducks. General references describing species of estuarine birds and some of their habits in Pacific Northwest estuaries include Gabrielson and Jewett (1940), Jewett et al. (1953), Eaton (1975), Salo (1975), Manuwal (1977), and Simenstad et al. (1979a). The most authoritative, quantitative information, that included in Wahl et al. (1981), encompassed northern Puget Sound and the Straits of Georgia and Juan de Fuca but seldom covered or differentiated bird assemblages in true estuarine channels.

Synthesis of these references and of pertinent coastal inventories (U.S. Dep. Interior 1971; Monroe et al. 1974; Kreag 1979a, b, c; Ratti 1979a, b; Roye 1979; Starr 1979a, b; Proctor et al. 1980; Beccasio et al. 1981) indicate that 59 species of birds are common to the region's estuarine channel habitats, 23 of which could be considered prevalent (abundant) (Table 7.1; Fig. 7.1, 7.2).

7.1 SHALLOW-PROBING AND SURFACE-SEARCHING SHOREBIRDS

Characteristic of their foraging on or within sediment surface layers, birds of this assemblage occupy shoreline environs constituting the boundaries between channel and other estuarine habitats. Comprising slightly more than 25% of the

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[5] I will refrain, however, from using the term "guild" because of the assumption of common exploitation of an investigator-defined resource (Root 1967; Jaksić 1981), opting instead for "assemblage," which is more broadly defined as a group of syntopic related taxa.

Table 7.1. Itemization and characteristics of birds common to estuarine channels of the Pacific Northwest, organized by assemblage.

Assemblage	Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
Shallow-probing and surface-searching shorebirds	Haematopus bachmani (American black oystercatcher)	M	E	O-B
	*Charadrius alexandrinus (Snowy plover)	M-B	R-E	O-B; Seasonal transient
	C. semipalmatus (Semipalmated plover)	M-B	R-E	O-B; Seasonal transient
	Pluvialis squatarola (Black-bellied plover)	M-B	R-E	O-B; Seasonal transient
	Numenius phaeopus (Whimbrel)	M-B	R-E	O-B
	Actitis macularia (Spotted sandpiper)	M-B	R-E	O-B; Seasonal transient
	*Limnodromus griseus (Short-billed dowitcher)	M-B	R-E	O-B
	L. scolopaceus (Long-billed dowitcher)	M-B	R-E	O-B
	Aphriza virgata (Surfbird)	M,S	M-E	O-B; Seasonal transient
	Arenaria interpres (Ruddy turnstone)	M,S	O-E	O-B; Seasonal transient
	*Calidris alba (Sanderling)	M-B	R-E	O-B; Seasonal transient
	*C. alpina (Dunlin)	M-B	R-E	O; Seasonal transient
	C. canutus (Red knot)	M-B	R-E	O
	*C. mauri (Western sandpiper)	M-B	R-E	O
	C. minutilla (Least sandpiper)	M-B	R-E	O-B
	Phalaropus lobatus (Red-necked phalarope)	M	M-E	O,F-PK; Seasonal transient
Waders	*Tringa melanoleuca (Greater yellowlegs)	M-B	R-E	F-B; Seasonal transient
	*Ardea herodias (Great blue heron)	M-B	R-E	O-PS
	Bubulcus ibis (Cattle egret)	M-B	R-E	F-PS
	Casmerodius albus (Great egret)	M-B	F-E	O-PS
	Egretta thula (Snowy egret)	M-B	R-E	O-PS

(continued)

Table 7.1. Continued.

Assemblage	Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
Surface and diving waterbirds	**Aechmophorus occidentalis* (Western grebe)	M	R-E	0-PS
	Podiceps auritus (Horned grebe)	M,S	R-E	F-PS; Seasonal transient
	P. grisegena (Red-necked grebe)	M,S	R-E	0-PS; Seasonal transient
	P. nigricollis (Eared grebe)	M,S	R-E	0-PK; Seasonal transient
	**Phalacrocorax auritus* (Double-crested cormorant)	M,S	R-E	0-PS
	**P. pelagicus* (Pelagic cormorant)	M,S	M-E	F-PS
	**Mergus merganser* (Common merganser)	M-B	R-E	0-PS
	M. serrator (Red-breasted merganser)	M-B	R-E	F-PS; Seasonal transient
	**Uria aalge* (Common murre)	M	M-E	0-PS; Seasonal transient
	Cepphus columba (Pigeon guillemot)	M	M-E	F-PS
	Cerorhinca monocerata (Rhinoceros auklet)	M	M-E	0-PS
	Brachyramphus marmoratus (Marbled murrelet)	M	M-E	F-PS
	Branta bernicla (Brant)	S,B	R-E	0-H; Seasonal transient
	**Anas platyrhynchos* (Mallard)	M-B	R-M	0, F-H; Seasonal transient; primarily roosting in habitat
	A. acuta (Northern pintail)	M-B	R-M	0, F-H; Primarily roosting in habitat
	A. crecca (Green-winged teal)	M-B	R-M	0, F-H; Seasonal transient; Primarily roosting in habitat
	**A. americana* (American wigeon)	M-B	0-E	0, F-H; Seasonal transient; Primarily roosting in habitat
	Aythya valisineria (Canvasback)	M-B	R-M	0, F-H; Seasonal transient; Primarily roosting in habitat
	A. marila (Greater scaup)	M-S	R-E	F-B; Seasonal transient

(continued)

Table 7.1. Concluded.

Assemblage	Taxa (common name)	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
Surface and diving waterbirds - cont'd.	*A. affinis (Lesser scaup)	M-S	R-E	O, F-B; Seasonal transient; Primarily roosting in habitat
	Bucephala clangula (Common goldeneye)	M-B	R-E	F-B; Seasonal transient
	B. albeola (Bufflehead)	M-B	R-E	F-B
	*Melanitta fusca (White-winged scoter)	M-S	R-E	F-B; Seasonal transient
	*M. perspicillata (Surf scoter)	M-S	R-E	F-B
Aerial-searching birds	Ceryle alcyon (Belted kingfisher)	M-B	R-E	O-PS
	Pandion haliaetus (Osprey)	M,S	R-E	F-PS
	*Haliaeetus leucocephalus (Bald eagle)	M,S	R-E	F-A
	*Larus glaucescens (Glaucous-winged gull)	M-B	R-E	F-B
	L. occidentalis (Western gull)	M-B	R-E	F-B
	L. californicus (California gull)	M-B	R-E	F-B; Seasonal transient
	L. delawarensis (Ring-billed gull)	M-B	R-E	F-B; Seasonal transient
	L. heermanni (Heermann's gull)	M-S	R-E	F-B; Seasonal transient
	*L. philadelphia (Bonaparte's gull)	M-S	M-E	F-PK
	*Larus canus (Mew gull)	M,S	M-E	F-PK; Seasonal transient
	*Sterna hirundo (Common tern)	M,S	M-E	O-PS; Seasonal transient
	*S. caspia (Caspian tern)	M,S	M-E	F-PS; Seasonal transient
	Pelecanus occidentalis (Brown pelican)	M	P-E	O-PS; Seasonal transient
	Stercorarius parasiticus (Parasitic jaeger)	M-B	R-E	F-PS, K; Seasonal transient

*Species prevalent in all Pacific Northwest estuarine channels.

[1] M = Mainstem; S = Subsidiary; B = Blind
[2] R = Riverine; O = Oligohaline; M = Mesohaline; P = Polyhaline; E = Euhaline
[3] O- = obligate; F- = facultative; B = benthivore; PS = piscivore; PK = planktivore; H = herbivore; I = insectivore; O = omnivore; K = kleptoparasite

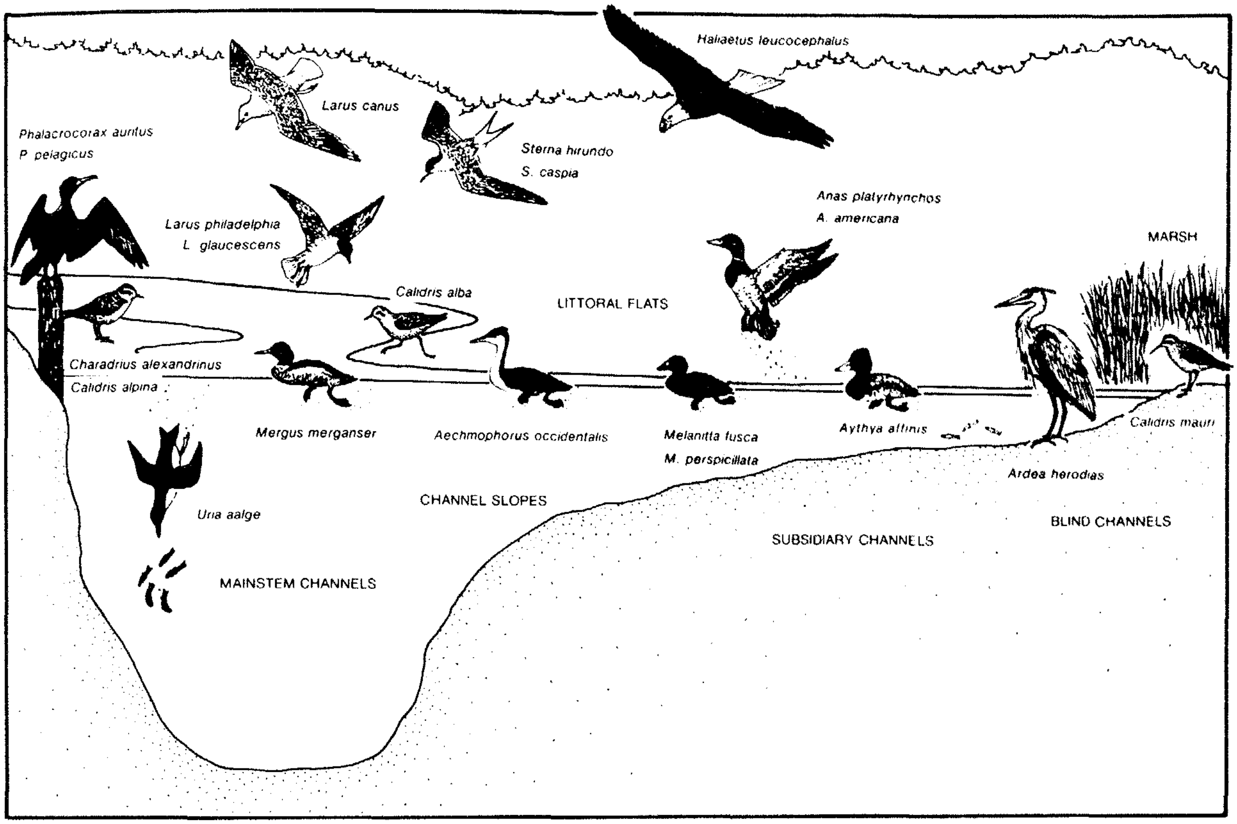


Fig. 7.1. Representative illustration of common bird assemblages of estuarine channels of the Pacific Northwest.

common species and five of the prevalent species (three families in the order Charadriiformes; Haematopodidae, Charadriidae, and Scolopacidae), these shorebirds are typically seen actively feeding in the substrate along the shoreline, particularly at high tide when littoral flat habitats, the preferred foraging habitat of most, are inundated. Due to the general lack of daylight minus tides between September and February, much of the fall-winter foraging by this assemblage is concentrated closer to and about channel shorelines. Some (American black oystercatcher, snowy plover, whimbrel, both dowitchers, dunlin, knot, sanderling) appear singly or in small, loosely associated groups while others (sandpipers, surfbird, ruddy turnstone) occur in dense, tightly associated flocks.

Considerable habitat partitioning results as a function of the heterogeneity of shoreline substrates. Thus, current and wave exposure which influences sediment characteristics of channel shorelines determines, to a large extent, the species composition of this assemblage. For example, black oystercatchers are typically found along rocky cliffs, headlands, and jetties in the euhaline region of those estuaries which possess this habitat (predominantly in Oregon); dunlins, western sandpipers, sanderlings, and knots appear commonly on exposed sand beaches in the lower reaches of the estuaries; and whimbrels and dowitchers characterize the more protected, inner bays and flats. Tidal fluctuations affecting the availability of preferred foraging habitats and microhabitats, however,

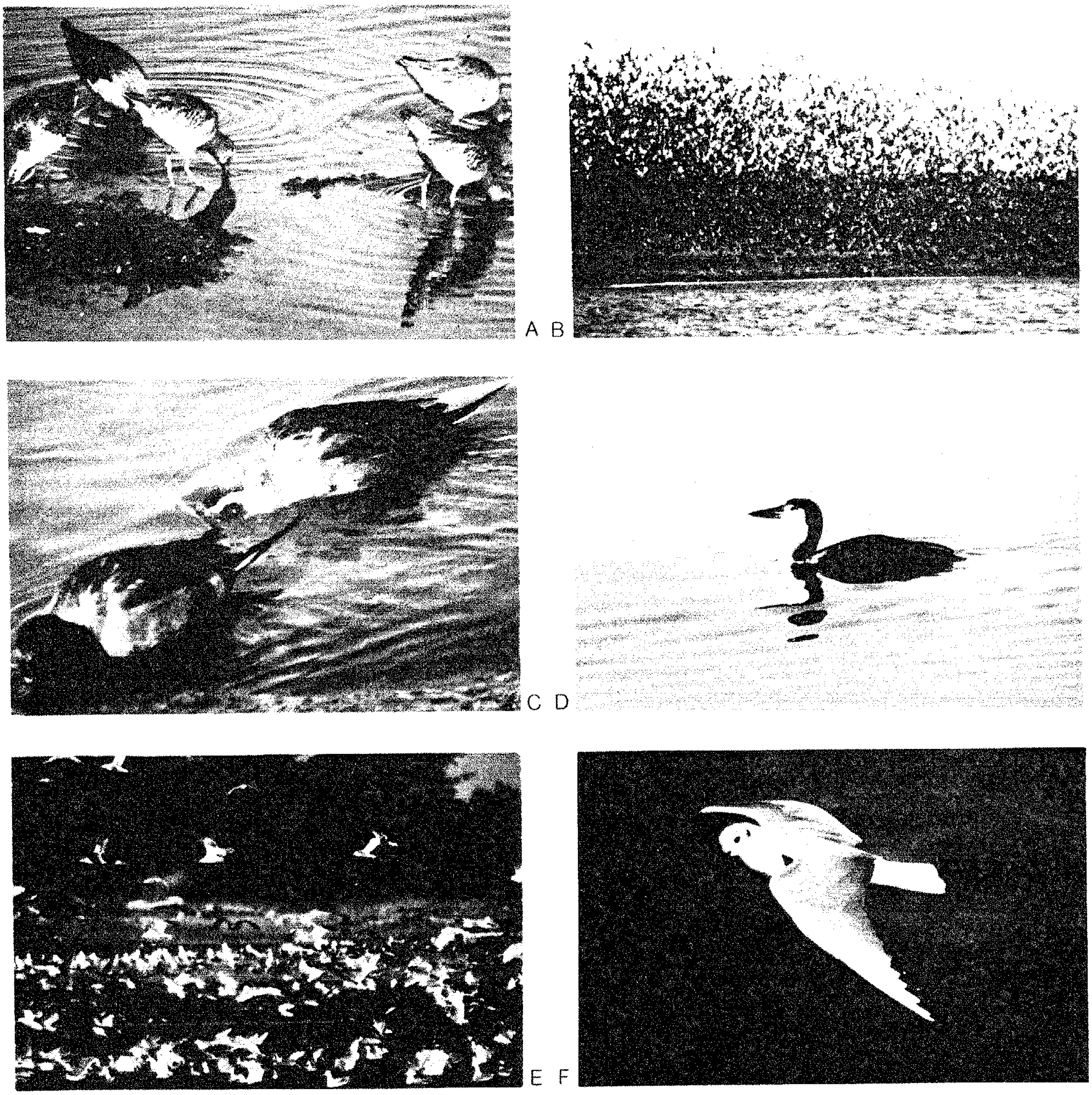


Fig. 7.2. Representative avifauna of estuarine channel habitats in the Pacific Northwest: A) feeding dowitchers; B) spring flock of western sandpipers, dunlins, and short-billed dowitchers; C) feeding male northern pintails; D) adult common loon (*Gavia immer*) in winter plumage; E) fall flock of California and Heermann's gulls; and, F) adult Bonaparte's gull in winter plumage. All photographs courtesy of Dr. Dennis Paulson, University of Washington.

induce considerable movement about the estuary and many species periodically frequent a diversity of habitats. As such, considerable spatial overlap in foraging space is imposed upon these shorebirds, which may be responsible for the evolution of diverse feeding behaviors and bill morphologies (Recher 1966).

Distribution of the assemblage throughout the region is relatively uniform with some exceptions (Beccasio et al. 1981). For example, snowy plovers are concentrated along the marine margins of the southern estuaries and dunlins appear more in the central coastal estuaries (i.e., Tillamook Bay, Willapa Bay, Grays Harbor), and, in general, the migratory species are more commonly encountered in abundance along the coastal estuaries than in the inland estuaries, which are more removed from the mainstream of the Pacific Flyway.

Approximately a third of the assemblage are migrants and their abundances typically reach maxima in spring (April-May) and fall (September-November), when they are migrating through the Pacific Northwest. Intermediate levels of abundance in the winter are associated with overwintering of some species in the estuaries. This variation is illustrated by the corrected aerial estimates of total shorebird abundances in Grays Harbor between September 1974 and October 1975 which fluctuated between averages of 65,833 in spring, 19,700 in summer, 52,500 in fall and 21,533 in winter (Smith and Mudd 1976a). Similarly, Jones and Stokes Associates, Inc.'s (in prep.) summary of their 1980-1981 CREDDP studies of the avifauna in the Columbia River estuary indicated densities of "peeps" (confined to the "key" species of dunlin, sanderling, and western sandpiper) as high as 378 km^{-2} in spring, 766 km^{-2} in fall, and 961 km^{-2} in winter, but peeps are virtually absent in the summer. Distribution of the assemblage was also broadest, essentially covering the whole estuary but concentrating on mid-estuary, in the spring and was more restricted in the fall. Significant overwintering was observed only at one site in the upper estuary, although "peep" density along a linear transect was estimated at 337 km^{-1} during that period.

7.2 WADERS

This assemblage, confined to birds that wade through shallow-water portions of the channel in search of invertebrate and fish prey, is composed of two groups which are quite different in distribution and ecology. Greater yellowlegs (Family Scolopacidae) forage along channel shores and shallows in water 5 to 10 cm deep and thus are found within channel habitats only when blind channels are tidally dewatered. Like many of the other shorebirds, they are seasonal transients who are most abundant in the region's estuaries during spring and fall migratory periods.

Great blue herons and egrets (Family Ardeidae) are estuarine residents that nest in wetland and adjacent upland, and forage in marshes, littoral flat, and channel habitats in waters ≤1 m deep. In channels, this includes shoreline and slope areas of mainstem channels and shallow subsidiary and blind channels throughout the estuaries. Great blue herons are distributed ubiquitously throughout the region while egrets are located principally in the coastal estuaries of northern California and southern Oregon (Beccasio et al. 1981). The density of herons in the Columbia River estuary peaked at almost 3 km^{-1} of linear transect surveyed during the summer months due to recruitment of young, but averaged between 1 and 2 km^{-1} during other seasons. Although distributed through all estuarine regions, herons tended to be concentrated in the central (i.e., oligohaline-polyhaline) region of that estuary. Part of this heterogeneity was due to the proximity to heron nesting colonies in the vicinity of Youngs Bay, Karlson Island, Ryan Island, and Brown's Island (Jones and Stokes Associates, Inc., in prep.). Much higher densities have been observed on the basis of linear shoreline; as many as 30 to 50 immature herons have been observed per linear km of shoreline in Grays Harbor during the summer (Dr. Dennis Paulson, Burke Mus., Univ. Wash. Seattle, WA; pers. comm.).

7.3 SURFACE AND DIVING WATERBIRDS

Another predominant bird assemblage found in estuarine channel habitats is that of the surface and diving waterbirds, which constitute over 40% of both the total common and prevalent species (Table 7.1) and include members of four families (Podicipedidae, grebes; Phalacrocoracidae, cormorants; Anatidae, waterfowl; and Alcidae, alcids). Unlike birds of the other assemblages, they utilize the channel water directly for both roosting and foraging. Although all roost on open water, during feeding some are confined to certain channel microhabitats by the constraints of their foraging behavior and prey preferences. Benthic herbivores (brant, mallard, northern pintail, green-winged teal, canvasback) and carnivores (double-crested cormorant, horned and red-necked grebes, greater and lesser scaup, common goldeneye, bufflehead, white-winged and surf scoters, pigeon guillemot) feed in shallow, channel slope areas where plant and animal food resources are within their respective diving ranges, while pelagic piscivores (pelagic cormorant, common and red-breasted merganser, Bonaparte's gull) and planktivores (eared grebe) tend to congregate along tidal fronts which congregate their prey.

Some species, particularly the piscivorous species, are further restricted to channels in the euhaline-mesohaline regions of the estuary. Smith and Mudd (1976a) illustrated the areal distribution of seabirds (including rhinoceros auklets, common murres, marbled murrelets, pigeon guillemots) in Grays Harbor to be confined to channel habitat in the outer estuary where water depth was greater than 6 m relative to MLLW (Fig. 7.3). Distributions of pelagic cormorant and surf scoter were similarly concentrated in lower and mid-estuary regions of the Columbia River estuary, while other species (mallard, American wigeon, and common merganser) tended to occur in the central and upper regions of that estuary (Jones and Stokes Associates, Inc., in prep.). In the case of high densities of western grebes and hybrid (glaucous-winged/western) gulls in the central portion of the estuary during the winter, seasonal aggregations not related to migrations into or out of the estuary have also been correlated to migratory concentrations of preferred prey such as longfin smelt.

As over two-thirds of the species in this diverse assemblage are seasonal migrants, their densities and the overall assemblage structure changes dramatically over the year. Most of the species migrate out of or through the estuary during spring and return in the fall, promoting density maxima during these periods. But, despite generally lower species richness, the numerical diversity (Shannon-Weaver H') of the assemblage can be high in the summer due to the more even distribution of individuals during nesting of residents, as has been documented in the Columbia River and other coastal estuaries (Edwards 1979; Crawford and Dorsey 1980; Jones and Stokes Associates, Inc., in prep.). Smith and Mudd (1976a) estimated waterfowl density along the two major channels in inner Grays Harbor to reach maxima of 426 individuals km^{-1} (linear transect) in April and 130-140 km^{-1} in September-November. At the same time, taxon richness ranged from 10 in January to 16 in April, was between 1 and 5 from May through August, and increased from 4 in September to 10 in December. The 1980-1981 CREDDP studies in the Columbia River estuary described total densities of this assemblage in open water habitats to range between 425 km^{-2} in spring, 637 km^{-2} in summer, 442 km^{-2} in fall, and 769 km^{-2} in winter, while mean numerical diversity (Shannon-Weaver H') and evenness (H'/H' max) respectively ranged from 1.06 and 0.60 in spring, 1.73 and 0.72 in summer, 1.97 and 0.76 in fall, to 1.61 and 0.67 in winter (Jones and Stokes Associates, Inc., in prep.). The spring data, however, consisted of only one, late census which did not survey any large flocks of migrants and may therefore be unrepresentative of this season.

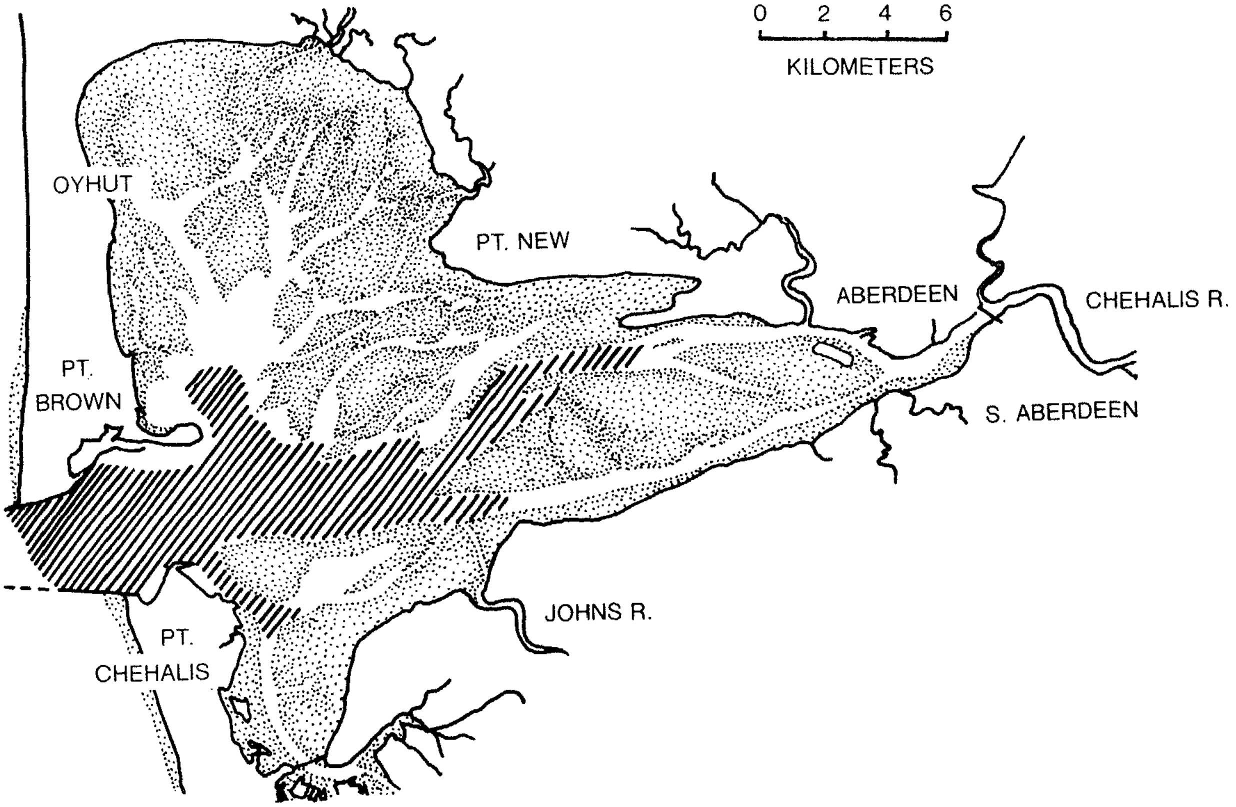


Fig. 7.3. Seabird (primarily rhinoceros auklets, common murres, marbled murrelets, and pigeon guillemots) distribution in Grays Harbor, Washington, October 1974 to September 1975; stippled area indicates littoral sand or mudflat habitat and hatched area indicates seabird occurrence (figure from Smith and Mudd 1976a).

7.4 AERIAL-SEARCHING BIRDS

Aerial-searching birds include both terrestrial (belted kingfisher, swallows, osprey, bald eagle) and waterbirds (gulls, terns, and brown pelican) which fly over and along channels while foraging for prey over, on, or just within the water surface. Waterbirds also roost on the surface.

Belted kingfishers, ospreys, and bald eagles all require perches in the proximity of their common foraging habitat and thus are less prevalent or absent over channels in large expanses of open water such as occur in the lower regions of many estuaries. In the Columbia River estuary, for example, the distribution and abundance of bald eagles is centered in the central region of the estuary through most of the year (Jones and Stokes Associates, Inc., in prep.). The proximity of foraging habitats to nesting sites may also restrict the effective distribution of these birds along the estuary.

Gulls and terns, however, are much more widely distributed through the estuaries as they rapidly cover broad expanses of open water during their feeding forays away from estuarine breeding colonies. Much of this wide aerial distribution is due to the relatively dynamic nature of their prey resources, such as macrozooplankton and small, schooling fishes which occur sporadically with shifting currents and tidal fronts throughout the estuary; tidal inundation and exposure of benthic and sessile organisms along channel shores also contributes to movement of gulls which prey upon these organisms.

While the terrestrial-associated birds of the assemblage are estuary residents, both mew gulls and the two terns are seasonal transients, although in opposite patterns. Mew gulls, like most of the waterfowl, migrate out of the region's estuaries during the summer. The maximum abundances recorded in Grays Harbor between October 1974 and September 1975 occurred in December though April (maximum of 1.4 km^{-1} along a channel transect in upper estuary in March) and the gulls were absent from May through July (Smith and Mudd 1976a). Jones and Stokes Associates, Inc. (in prep.) reported maximum mew gull densities of 193 km^{-2} in fall 1980 and 400 km^{-2} in winter 1980-1981 in the Columbia River estuary. Common and Caspian terns are summer immigrants into the large coastal estuaries and Caspian terns breed in large estuarine colonies throughout the region (Beccasio et al. 1981). High densities of common terns occur in Grays Harbor in May (2.6 km^{-1} along channel transect in upper estuary) and equally so in September. Caspian terns, which breed on Whitcomb Island in the lower estuary from May to October (Penland 1976), are most abundant (18 km^{-1}) in channel habitats during July when food requirements for fledglings are at a maximum (Smith and Mudd 1976a). The density of Caspian terns in the Columbia River estuary reached $\sim$93 km^{-2} during summer 1980 censuses by Jones and Stokes, Associates, Inc. (in prep.).

As the "California" subspecies, the brown pelican is an endangered species which occurs in small aggregations of immatures as far north as Grays Harbor and is a fall (August-September) occupant of the euhaline regions of a number of the coastal estuaries to the south (Willapa Bay, Columbia River, Coquille, Chetco and Humbolt Bay) (Beccasio et al. 1981).

CHAPTER 8

MAMMALS OF ESTUARINE CHANNELS

Terrestrial, aquatic, and marine mammals utilize estuarine channel habitats to varying extents and for various purposes. Although members of adjacent wetland or upland communities, terrestrial mammals periodically forage along the shoreline boundaries with channel habitats. Aquatic mammals actually utilize channels for much of their principal foraging. Compared to terrestrial and aquatic mammals, marine mammals occupy channels extensively, some exclusively, for foraging, movement, migration, resting, and reproduction. Other than man, they constitute the predominant proportion of the tertiary consumer level (see Chap. 9).

One terrestrial (procyonid), four aquatic (one each castorid, cricetid, capromyid, and mustelid), and four marine (all pinnipeds) mammals are common to channel habitats in Pacific Northwest estuaries (Fig 8.1; Table 8.1). In addition to these, other marine mammals such as orca or killer whale (*Orcinus orca*), har-

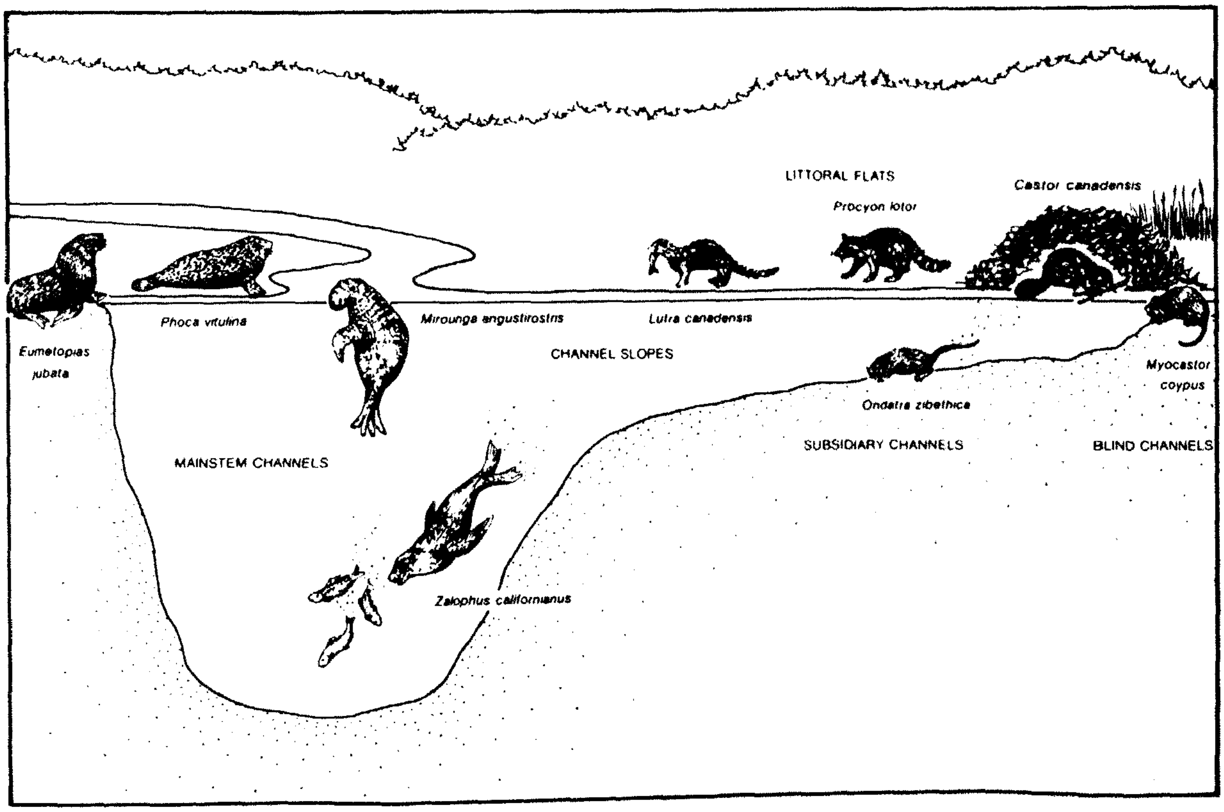


Fig. 8.1. Representative illustration of common mammal assemblages of estuarine channels of the Pacific Northwest.

Table 8.1. Itemization and characteristics of terrestrial, aquatic, and marine mammals common to estuarine channel habitats in the Pacific Northwest.

Taxa	Channel habitats[1]	Salinity associations[2]	Relevant life history characteristics[3]
Terrestrial:			
Procyon lotor (Raccoon)	S,B	R-E	F-EC
Aquatic:			
Castor canadensis (American beaver)	S,B	R-O	O-H
Ondatra zibethica (Muskrat)	S,B	R-M	O-H
Myocastor coypus (Nutria or coypu)	S,B	R-M	O-H
Lutra canadensis (Canadian river otter)	M-B	R-E	O-EC
Marine:			
Eumetopias jubata (Northern sea lion)	M,S	R-E	F-PC
Zalophus californianus (California sea lion)	M,S	R-E	F-PC
Phoca vitulina richardi (Harbor seal)	M	R-E	F-EC
Mirounga angustirostris (Northern elephant seal)	M	P-E	F-PC

[1] M = Mainstem; S = Subsidiary; B = Blind.

[2] R = Riverine; O = Oligohaline; M = Mesohaline; P = Polyhaline; E = Euhaline.

[3] O- = obligate; F- = facultative; EC = epibenthic carnivore; PC = pelagic carnivore; H = herbivore.

bor porpoise (Phocoena phocoena), gray whale (Exchrichtius robustus), and minke whale (Balaenoptera acutorostrata) have been reported sporadically in the region's estuaries. As with the avian assemblages, comprehensive documentation of mammal assemblages in the region's estuaries is relatively recent and limited to the coastal estuaries in the vicinity of the Columbia River, e.g., Grays Harbor, Willapa Bay, Columbia River estuary, Tillamook Bay, and Netarts Bay (Smith and Mudd 1976b; Howerton et al. 1980; Dunn et al. 1981; Beach et al. 1981) and in the less-estuarine environs of northern Puget Sound and the Strait of Juan de Fuca (Everitt 1980; Everitt et al. 1980). Quantitative (population sizes and dynamics) studies of terrestrial and aquatic mammals in Pacific Northwest estuaries are rare or nonexistent. Assemblage accounts of distributions and population assessments of marine mammals, however, have been available since the 1940's (Scheffer and Slipp 1944, 1948; Manzer and Cowan 1956; Cowan and Guiguet 1965; Bigg 1969; Pike and MacAskie 1969).

Extensive population biology and ecology studies of pinnipeds in estuarine habitats have occurred during the past two decades (Pearson 1969; Pearson and Verts 1970; Mate 1975; Brown and Mate 1979; Calambokidis et al. 1978, 1979; Brown 1980; Bowlby 1981; Roffe 1981). Becassio et al. (1981) included these common mammal species in their comprehensive ecological inventory of the Pacific Coast.

8.1 TERRESTRIAL MAMMALS

Raccoons are one of the few terrestrial mammals which frequents channel habitats in conjunction with their principal use of adjacent littoral flat, salt and freshwater marsh, and riparian swamp habitats. Utilization of the channel is almost exclusively confined to foraging for shallow-water fauna. Feeding periodicity and intensity is principally a function of tidal cycles. Although raccoons have been observed feeding during both day- and nighttime, they appear to prefer nighttime low tide periods when they can safely forage across littoral flats (Smith and Mudd 1976b; Dunn et al. 1981). Thus feeding activity tends to be seasonal in nature, i.e., more intensive in fall and lowest during spring. Raccoons in the Columbia River estuary have been observed through all estuarine regions, from the euhaline region of the Ilwaco Channel to the marsh channels of Puget Island, although peak observations occurred in the complex system of islands and channels in Cathlamet Bay (Dunn et al. 1981).

8.2 AQUATIC MAMMALS

American beaver are common only in small subsidiary and blind channels which intersect freshwater marsh and riparian habitats, particularly sitka willow (Salix sitchensis), creek dogwood (Cornus stolonifera), or similar habitats in riverine-mesohaline marshes such as the Cathlamet Bay area of the Columbia River estuary (Wash. Dep. Game 1981). Extremely small channels may be dammed and permanently occupied (denning and resting) by beaver in some instances.

Muskrat have a broader spectrum of habitat utilization than beaver, being more common in the sedge (Carex spp.), horsetail (Equisetum spp.), and bulrush (Scirpus sp.) salt- and freshwater habitats in addition to the riparian habitats occupied by beaver (Smith and Mudd 1976b; Wash. Dep. Game 1981). Denning and resting, however, also occur in close association with steep-sided estuarine (principally subsidiary and blind) channels adjacent to or in these habitats and, as such, constitute critical habitats for this species (Dunn et al. 1981). Feeding and other activities almost always occur less than 60 m from the channel den and principally during high tide and nocturnal hours, perhaps to facilitate access to feeding areas along the channel banks and to minimize vulnerability to predators.

Nutria habitats overlap somewhat with those of American beaver in their occupation of marsh and riparian swamp habitats. In the Columbia River estuary the most common features of nutria habitat are complex steep-sided tidal channel systems within extensive high marshes (principally reed canarygrass, Phalaris arundinacea/cattail, Typha sp.), where their principal forage plants (see Section 9.1) are readily available (Dunn et al. 1981). Unlike muskrat, nutria appear to maintain extensive home ranges (∿0.4 km^2) containing several habitats and to have no seasonal or diel periodicity to their activity patterns.

Among the terrestrial and aquatic mammals the Canadian river otter undoubtedly maintains the highest utilization of estuarine channels and is the only species which commonly occupies mainstem channels. Although most observations of river otter in the Columbia River estuary were correlated with sitka spruce (Picea sitchensis) and/or sitka willow-dominated forest, otter were typically associated with complex channel networks of tidal creeks and sloughs (subsidiary and blind channels) which offered easily accessible, concentrated prey resources (clams, crayfish, and demersal fishes) during periodic tidal dewatering (Dunn et al. 1981). In Grays Harbor, river otter have been observed only in tributary rivers and streams, although it is assumed that they utilize the open waters of the estuary (mainstem channels) to travel between tributaries (Smith and Mudd 1976b). Otters also are relatively adaptable to the presence of man as long as critical habitat and food resources are maintained; Cowan and Guiguet (1965) considered them the most numerous aquatic mammal in Vancouver (B.C., Canada) Harbor.

8.3 MARINE MAMMALS

Harbor seals and California and northern sea lions are both common and abundant in Pacific Northwest estuaries although densities fluctuate seasonally as a function of feeding and breeding migrations (Mate 1975). Northern elephant seals are less abundant in the region and are more concentrated seasonally in the southern extreme of the region. While all four species occur frequently in coastal estuaries, northern elephant seals and California sea lions tend to be less abundant in the inland estuaries of Puget Sound.

Northern sea lions are most abundant in the region during the non-breeding season between late fall and early spring and, except for a small population along the outer coast during the summer (Everitt and Jeffries 1979), are usually absent from the region from May through July. Total counts of northern sea lions in Washington in 1976 and 1978 peaked at ∿450 in February-March and at ∿600 in September-October (Everitt et al. 1980). But Beach et al. (1981) indicated that northern sea lion populations in 1981 varied considerably among three haulout sites in the vicinity of the Columbia River estuary; while occupation of the south jetty site at the mouth of the river was concentrated between January and May, maximum abundance at Tillamook Head, Oregon, occurred in May and June and did not occur at Three Arch Rocks until October-November. Much of this variation appears to be associated with shifts in preferred foraging habitat and location along the coast during the summer and a potential movement of sea lions into inside waters during the winter months (Everitt et al. 1980). Occupation of coastal estuaries often coincides with predictably high concentrations of prey, such as eulachon and spring chinook salmon spawning migrations through the Columbia River estuary in winter and spring (Beach et al. 1981). Movement in and out of the estuary must be relatively dynamic during this period, as no haulout areas are reported to occur within the estuary.

California sea lions also occur in Pacific Northwest estuaries during the non-breeding season between October and May, when they move northward from breeding sites at and south of San Miguel Island, California. They follow the same general abundance distribution pattern as the northern sea lion but are generally more abundant in coastal estuaries and less abundant in inland waters (Everitt et al. 1980; Beach et al. 1981). Everitt et al. (1980), however, reported extended hauling out of California sea lions at haulout areas in the Port Gardner area of Puget Sound, a significant expansion of their utilization and abundance in inside waters.

In the Columbia River estuary foraging California sea lions are numerous throughout the estuary during the spring fish migrations, occurring as far upriver as Bonneville Dam, although no haulout sites have been documented to occur within the confines of the estuary. This sea lion is credited with some fish and fishing gear damage in the fall and is considered to be the major cause of gear damage in the lower river and estuary during the 1981 winter season (Beach et al. 1981).

Of all marine mammals, the Pacific harbor seal is the most ubiquitous and abundant and is the only breeding pinniped in the region (Scheffer and Slipp 1944; Everitt et al. 1980). The State of Washington is estimated to provide refuge to over 7,000 harbor seals (Everitt et al. 1980). Beach et al. (1981) estimated 5,000-6,000 harbor seals present in their study area between Grays Harbor and Netarts Bay, including at least 55 haulout sites in the five major estuaries

(Fig. 8.2). Beccasio et al. (1981) illustrated similarly uniform distribution south to Humboldt Bay.

Of all the pinnipeds, harbor seals are the most estuarine-oriented, even in the confined waters of Puget Sound where they can be observed moving up the smallest of estuarine channels during flood tide. Local movement, however, is common as a result of foraging and reproduction demands (Brown and Mate 1979; Everitt et al. 1981). Movement into the Columbia River estuary, for example, occurs from adjoining coastal estuaries during late winter coincident with the eulachon migration, and maximum seal abundance (1,000-1,500) is sustained through the spring. Seals apparently follow the eulachon as far upriver as Longview, Washington, but abandon the upriver haulout sites and fade back into the estuary until late spring (Beach et al. 1981). During the pupping season from April to July the population diffuses out of the Columbia River estuary into peripheral areas of Willapa Bay, Grays Harbor, and Tillamook Bay (Fig. 8.3).

Northern elephant seals are the least common pinniped frequenting estuarine channels and usually constitute solitary individuals which range north of their breeding locations (Farallon Islands, California south to Baja, Mexico) from spring through fall but which may occur in the Pacific Northwest throughout the year (Everitt et al. 1980). All observations of live elephant seals have been at the mouths of coastal estuaries or in inland marine waters, and only one haulout area (Trinidad Rock, California) has been identified in the region (Beccasio et al. 1981).

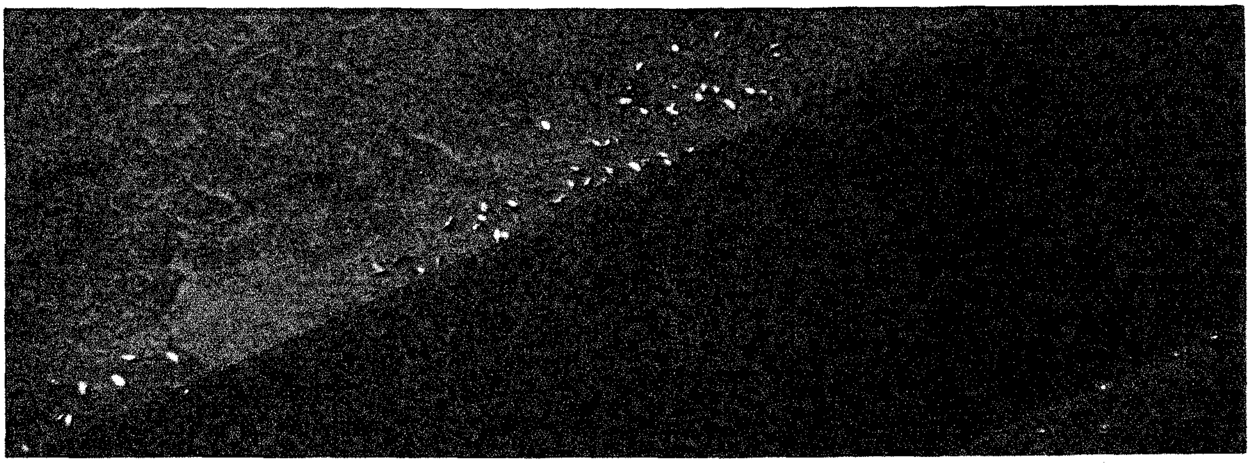


Fig. 8.2. Pacific harbor seal haulout site along channel in Willapa Bay, Washington, June 1980 (photo courtesy of Steven Jefferies, WSDG).

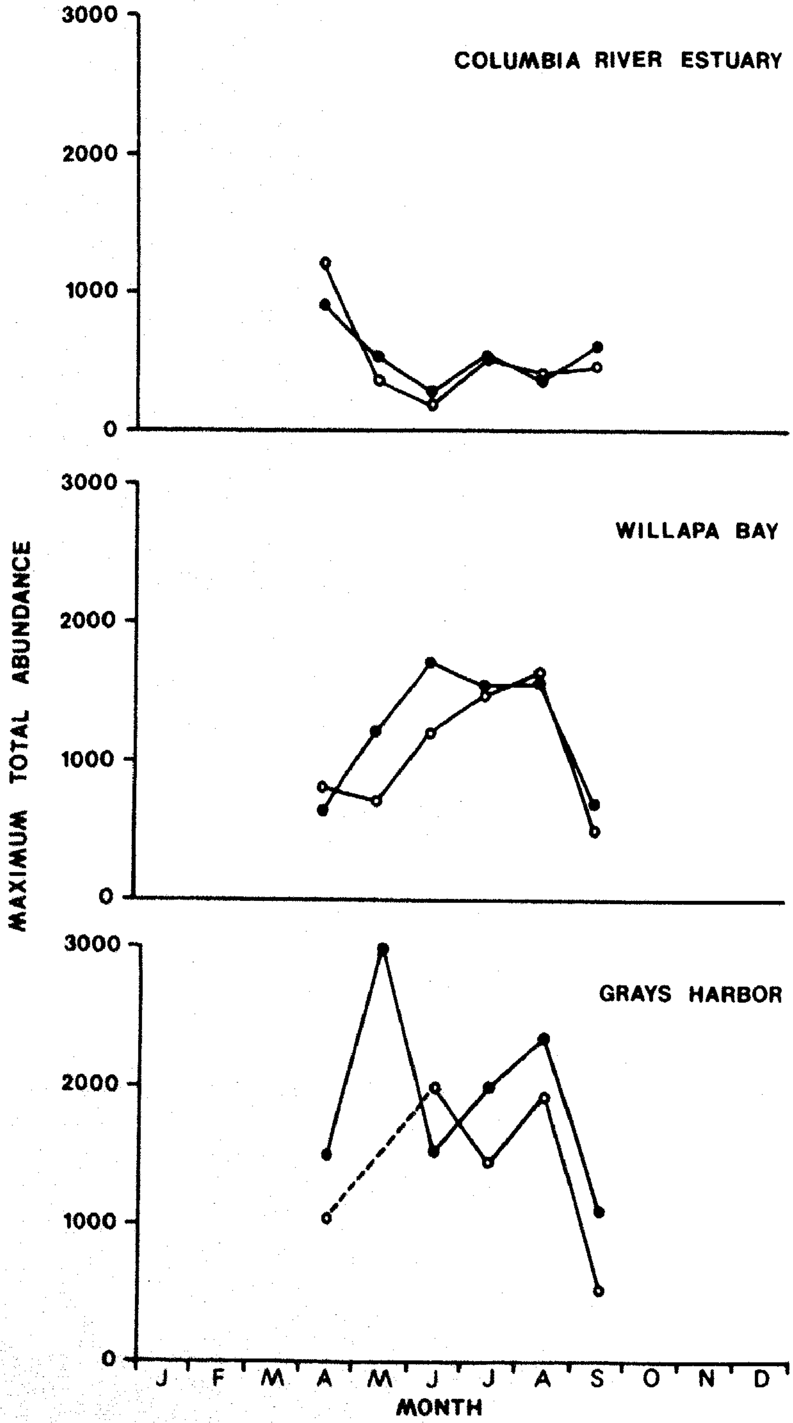


Fig. 8.3. Maximum total abundance (aerial counts) of Pacific harbor seals at haulout sites in three of Washington's coastal estuaries in 1980 (open symbols) and in 1981 (closed symbols) (figure redrawn from data of Beach et al. 1981).

CHAPTER 9

TROPHIC AND COMMUNITY ECOLOGY OF ESTUARINE CHANNELS

Previous chapters have presented physiochemical and biological characteristics of estuarine channels as distinct and disassociated when, in fact, flora and fauna are integrally linked through trophic and other ecological relationships and are affected in a variety of ways by the abiotic influences on the community. Quite often these functional relationships are so complex that the mechanisms responsible for the distribution, standing stock, or behavior of an organism cannot be isolated. But even without such definitive understanding of causal mechanisms, it can be argued that, within the physical spectrum of estuarine channel habitats, faunal assemblages are deterministically structured. These assemblages and the temporal and spatial changes they undergo every year are maintained by a suite of functional, ecological relationships including, but not limited to, trophic or food web linkages, competition and predation influences, reproductive requirements, and basic physiological constraints. In addition, many of these structuring influences can be manifested through interactions with adjacent habitats. That is, just as an estuarine channel organism can not exist in that habitat without interacting with other organisms, there are inumerable bonds between habitats which influence the character of each; these bonds cannot be measurably perturbed without altering the result (i.e., assemblage structure and/or standing stock) of the connection. Identifying these integral relationships can also illuminate the potential impact of altering them within and without the habitat for the everpressing need for development and manipulation of estuarine channels.

9.1 PRINCIPAL PATHWAYS OF ENERGY FLOW THROUGH INTERNAL FOOD WEBS

Unlike many distinguishable estuarine communities which have been studied extensively, particularly those of the Atlantic coast of North America (Teal 1962; Pomeroy et al. 1972 Nixon and Oviatt 1973; Kelly 1976; Kremer and Nixon 1978; Albanese 1979) and Gulf of Mexico (Day et al. 1973; Hopkinson and Day 1977), there is no quantitative definition of carbon or energy flow through Pacific Northwest estuarine food webs, much less of the particular channel component. Simenstad et al. (1979a) provided generalized, semi-quantitative diagrams of food web relationships within littoral, shallow sublittoral, and neritic habitats of northern Puget Sound and the Strait of Juan de Fuca but did not specifically distinguish estuarine channel habitats. Only Northcote et al.'s (1979) generalized food webs leading to fishes of the Fraser River estuary provide relative evaluation of trophic carbon flow among consumers inhabiting channel habitats. In addition to these sources, diverse literature on feeding mechanisms and behavior and prey composition of consumer fauna is available for several estuarine channels.

Benthic infauna and sessile epifauna are principally primary consumers via burrowing (i.e., oligochaetes Nephthys spp., polychaete annelids), surface deposit feeding (i.e., Macoma spp. bivalves and Corophium spp. amphipods), or suspension feeding (i.e., Saxidomus giganteus and Mytilus edulis bivalves). Jumars and Fauchald (1977) have further partitioned polychaete feeding strategies by sessile, discretely motile, and motile animals, the latter of which include carnivorous taxa such as *Nephthys* and *Eteone*. While some organisms (i.e., *Acmaea* spp. gastropods) are assumed to graze discriminately upon microalgae, it has commonly been assumed that most capture and ingest food particles simply on the basis of size as a function of filtering or other feeding morphologies. It has become readily apparent, however, that selective ingestion of food particles occurs, perhaps on the basis of chemical and/or physical composition (i.e., Tietjen and Lee 1977 for nematodes; Fauchald and Jumars 1979 for polychaetes), and that "food" can be composed of a combination of benthic microalgae, detritus, pelagic phytoplankton, and meiofauna. More recent studies have indicated that observed particle selection patterns are more the result of the mechanics of particle handling than of behavioral responses to particle characteristics (Jumars et al. 1982; Taghon 1982). DOC, as well, may be assimilated in the feeding process or many deposit feeders (Stephen 1967; Steward 1979; Levinton 1980). The resulting finite partitioning of food resources explains, within the constraints of temperature and salinity tolerances, much of the disparate structuring of benthic infauna assemblages and standing stock (see Section 5.1) as a function of sediment grain size, stability, and organic content (Sanders 1959).

Motile epifauna are principally benthic carnivores preying upon benthic infauna or sessile epifauna. Of the nine representative species (Table 5.2), two asteriods are obligate feeders on sessile bivalves, gastropods, barnacles, and sea urchins; two crabs are facultative carnivores on everything from benthic infauna, including meiofauna, to fish; and three shrimp species are obligate meiofauna carnivores. Only two species, the crayfish *Pacificastacus leniusculus*, and hermit crabs (*Pagurus* spp.), are, by their detritivory, primary consumers.

Although there is very little specific prey composition or feeding behavior information on these consumers in estuarine channels habitats, the diets of crangonid shrimps and cancrid crabs, the principal invertebrate secondary consumers in the community, have been examined from several coastal estuaries. Preliminary analyses of the stomach contents of *Crangon franciscorum* collected from different locations of the Columbia River estuary in June 1981 (C. Simenstad, Fish. Res. Inst., unpubl. data) indicate that at that time *C. franciscorum* was preying primarily on infauna and epifauna, including polychaete annelids, *Corophium* spp. amphipods, and the harpacticoid copepod *Scottolana canadensis*. There was little difference in diet among the four locations from which shrimp were examined. Three crangonids from Grays Harbor were also carnivorous on benthic infauna (Armstrong et al. 1982). *C. franciscorum* was found to feed principally on polychaete annelids (15.4% frequency of occurrence) and unidentified crustaceans (14.5%), while *C. nigricauda* and *C. stylirostris* had preyed upon crustaceans (12.7% and 11.5%, respectively) and small bivalve molluscs (19.0% and 7.7%, respectively). Although not evident in these data, *C. franciscorum* may also be a major predator on mysids (i.e., *N. mercedis*), as has been reported in the Sacramento-San Joaquin Rivers estuary (Siegfried 1982).

Prey composition of Dungeness crabs in Grays Harbor varied according to predator size, diel and seasonal cycles, and location in the estuary. In general, however, crabs <60 mm carapace width preyed primarily upon bivalve molluscs (*Tellina* spp., *Mya arenaria*, *Cryptomya californica*, *Macoma* spp., Cardiidae) and small crustaceans (amphipods, harpacticoid copepods, tanaids). Intermediate-sized crabs between 61 and 100 mm carapace width preyed equally upon small crustaceans, fish (lingcod, Pacific sanddab, Pacific sand lance, Pacific herring, Pacific tomcod, sand sole, shiner perch, longfin smelt, Pacific staghorn sculpin), and larger crustaceans (*Crangon* spp.; mud shrimp, *Callianassa californiensis*; Dungeness crab), and less so on bivalve mollusks. Large crabs >100 mm carapace width preyed predominantly upon fish, less on small crustaceans, and measurably less on large crustaceans and bivalves.

Although there is considerable variation in opinion about food preferences (Coull 1973), epibenthic zooplankton can probably be characterized as detritivores, as is often illustrated by their prominence in detritus accumulation areas such as the null zone (see Section 2.5.1). As such, they may play a critical role in the initial biological (fragmentation) conditioning of detritus (see Section 4.4) Harpacticoid copepods, in particular, have been found to rely heavily upon heterotrophically-produced carbon in the form of bacteria associated with detritus (Provasoli et al. 1959; Brown and Sibert 1977; Sibert et al. 1977b; Rieper 1978; Vanden Berghe and Bergmans 1981 among many). Considerable species-specific variability in food preferences may exist, possibly reflecting divergent functional (i.e., mandible) morphology and behavior (Marcotte 1977 and pers. comm.; Vanden Berghe and Bergmans 1981).

This characterization as specialists, in terms of nutritional preferences and requirements and the ability to utilize specific foods, may explain the often extreme fluctuations in epibenthic zooplankton assemblage structure observed in very dynamic estuaries such as the Columbia River (Houghton et al. 1980). Some prominent taxa, particularly Eurytemora affinis, can effectively feed on both detritus and phytoplankton, and it has also been suggested further that algal cells may actually contribute some trace metabolite necessary for normal egg production (Heinle et al. 1977). The presence of protozoa in association with the detritus may also form a critical link between the detrital POC and assimilation pathways of epibenthic copepods. Mysids such as Neomysis mercedis may, in addition to being detritivores and phytoplankton grazers, be carnivores. Although they are reported to consume primarily diatoms in the Sacramento-San Joaquin estuary (Kost and Knight 1975), Houghton et al. (1980) illustrated that N. mercedis in the Columbia River estuary fed opportunistically upon meiofauna and zooplankton (cladocerans, cyclopoid, harpacticoid, and calanoid copepods; rotifers) which were numerically prominent within the epibenthic region. This feeding mode was also verified by Siegfried and Kopache (1980), who found that, although not a particularly active predator, N. mercedis in the Sacramento River estuary derived >80% of its energy via carnivory on rotifers and copepods; direct herbivory appeared, in fact, to be of importance only during the spring diatom bloom. Wilson (1951) described N. mercedis in the Nicomekl and Serpentine Rivers Estuaries as feeding on both plant (diatoms, dinoflagellates, blue-green algae, vascular plant detritus) and animal matter (copepods and mysids). Johnson (1981) also describes the trophic role of N. mercedis in British Columbia estuarine channel habitats.

Estuarine pelagic zooplankton and neuston, perhaps reflecting the lower temporal and spatial diversity of available food resources in the water column as compared to benthic and epibenthic environs, illustrate more limited feeding strategies. Most are suspension feeders (Davis 1949; Poulet 1973; Richman et al. 1977; Lonsdale et al. 1979), although some omnivorous and carnivorous taxa are also prominent (Anraku and Omori 1963; Gauld 1966; Mullen 1977). In the case of the Pacific Northwest estuaries, predominant zooplankters include both herbivores (i.e., Eurytemora spp., Pseudocalanus spp., and Corycaeus anglicus) and omnivores (Acartia spp.), which themselves may be trophically linked (Hodgkin and Rippingale 1971).

Next to the avian assemblages, demersal fishes illustrate the most diverse spectrum of food web linkages and trophic levels in the habitat. This includes a few primary consumers (i.e., common carp feed considerably upon algae and other plant material as well as detritus; Wydoski and Whitney 1979), many secondary consumers and some species (i.e., dogfish, lingcod) which could be considered tertiary consumers although they are, in turn, susceptible to predation by other tertiary consumers such as marine mammals and, of course, man. Some species may, throughout the ontogenetic changes in feeding behavior, encompass several trophic levels and prey assemblages; white sturgeon, for instance, are reported to consume everything from epibenthic zooplankton as juveniles to salmon and house cats (a prime illustration of interhabitat linkages!) as adults. Among the representative species (Table 6.1) facultative epibenthic benthivores (17 species; 40%) and facultative epibenthic planktivores (12; 28%) predominate, followed by obligate epibenthic benthivores (5; 12%), obligate epibenthic planktivores (4; 9%), omnivores and parasites (2; 5%), and facultative meiobenthic benthivoes (1; 2%). This composition changes, of course, with seasonal changes in assemblage structure and with growth and development of resident species.

Reflecting the relative simplicity of their prey resources, pelagic fishes also illustrate less diverse feeding strategies than the demersal assemblage. Of the representative species (Table 6.2), all but two are primarily planktivorous, with only cutthroat trout and Dolly Varden exploiting other fishes. Two thirds (24) of the species are obligate pelagic planktivores, including two-thirds of these (16) which occur only as pelagic larvae. Four each (11%) are facultative pelagic planktivores or epibenthic planktivores and two each (6%) are obligate epibenthic planktivores or facultative pelagic piscivores. While the dominant zooplankton taxa comprise the principal prey resources of the planktivores, considerable size- or taxa-selective predation characterizes individual species and life history stages.

This was effectively illustrated by Johnson's (1981) detailed examination of the diets of three prominent pelagic planktivores in Yaquina Bay--juvenile northern anchovy, topsmelt, and surf smelt--relative to predation rates upon Acartia californiensis. When foraging in the water column, juvenile anchovy were highly selective toward the larger female A. californiensis and A. clausi, Eurytemora affinis, and the cladoceran Podon; surfsmelt reflected similar feeding selectivity while topsmelt reflected even greater selectivity upon predominantly female A. californiensis and both sexes of A. clausi. Considering the overall diets of these three planktivores, adult female A. californiensis composed 34.1% of the total number and 53.6% of the A. californiensis fraction.

The five species of juvenile salmon, whose food habits have been studied extensively (summarized in part by Levy and Levings 1978; Levy et al. 1979; Northcote et al. 1979; Levy and Northcote 1981; Durkin 1982; Healey 1982; and Simenstad et al. 1982b), also illustrate the varied prey resource utilization patterns which have evolved among congeneric taxa. Juvenile pink salmon occupy shallow sublittoral habitats for very short periods (days) before moving rapidly to pelagic channel or neritic habitats, feeding predominantly upon calanoid copepods and larvaceans. Contrastingly, juvenile chum salmon typically occupy shallow sublittoral habitats, especially sand-eelgrass, for several weeks feeding upon epibenthic zooplankton, particularly harpacticoid copepods and gammarid emphipods; upon growing to 50-60 mm FL, the juvenile chums also shift to pelagic channel or neritic habitats where they feed upon calanoid copepods, decapod larvae, and larvaceans. Juvenile coho salmon feed principally upon gammarid amphipods during their relatively brief occupation of shallow sublittoral habitats, particularly exposed gravel beaches, and upon decapod larvae and euphausiids after moving into eplagic or neritic habitats. Surprisingly little is known about the estuarine foraging behavior or prey composition of juvenile sockeye salmon due to their rapid emmigration through estuarine and nearshore marine habitats. Juvenile shrimp and euphausiids have been reported as the prey of juvenile sockeye migrating out of Puget Sound. Small juvenile chinook salmon tend to utilize shallow sublittoral, salt marsh, or mudflat habitats early in their estuarine residence, and feed upon gammarid emphipods, cumaceans, and emergent and drift insects. Upon growing larger or upon entering the estuary at a larger size as smolts (60-70 mm FL), they move into pelagic or neritic habitats but continue to feed upon drift insects, as well as decapod and fish larvae. Extremely selective foraging is also often evident within these broad prey categories. For example, in shallow sublittoral habitats juvenile chum salmon tend to feed on a narrow spectrum of harpacticoids >75 µm in length and, at least within Puget Sound, particularly the species *Harpacticus uniremis*. When in the pelagic habitats, they appear to select relatively rare but very large (>2 mm in length) calanoid copepods such as *Calanus* spp. and *Epilabidocera* spp. instead of other, more numerous but smaller calanoid (i.e., *Pseudocalanus* sp.) and cyclopoid (i.e., *Corycaeus* spp.) copepods (Simenstad et al. 1980). Several of the other species of juvenile salmon show similarly selective foraging in estuarine channels (Table 9.1).

Food habits data addressing the region's bird fauna which specifically occurs in estuarine channel habitats is almost non-existent and essentially limited to semi-qualitative data from Grays Harbor (Salo 1975; Smith and Mudd 1976a). Food web relationships of more marine/coastal bird assemblages have been summarized by Simenstad et al. (1979a) in their synthesis of nearshore and neritic habitats of the northern Puget Sound and Strait of Juan de Fuca ecosystem. Of the four syntopic species of marine diving birds examined by Scott (1973) in the vicinity of Yaquina Bay, two (common murre and Brandt's cormorant) may have acquired

Table 9.1. Principal preferred prey taxa of juvenile salmon in Pacific Northwest estuaries based on literature and other stomach contents data sources.

Juvenile salmon species	Size class (mm,FL)	Preferred prey taxa
Oncorhynchus gorbuscha Pink salmon	40-60	Calanoid copepods, *Pseudocalanus* spp. Larvaceans *Oikopleura* sp.
O. keta, chum salmon	35-55	Harpacticoid copepods *Harpacticus uniremis* Gammarid amphipod *Corophium* spp. Cumacean *Cumella vulgaris*
O. kisutch, coho salmon	>55	Calanoid copepods *Calanus* spp., *Epilabidocera* Gammardi amphipods *Eogammarus* spp. *Corophium* spp. Calanoid copepods *Eurytemora* sp., *Calanus* sp.
O. nerka, sockeye salmon	45-91	Adult insects Dipterans, Homoptera Euphausiids *Thysanoessa* spp.
O. tshawytscha, chinook salmon	35-75	Chironomid larvae and pupae Gammarid amphipods *Eogammarus* spp., *Corophium* spp., *Anisogammarus* spp. Cumaceans *Cumella vulgaris* Isopods *Gnorimosphaeroma oregonensis*
	>75	Adult insects Diptera, Homoptera Mysids *Neomysis mercedis* Larval fish *Clupea harengus pallasi*, *Hypomesus pretiosus*, *Engraulis mordax*

a portion of their diet from within estuarine habitats; coincidentally, it was these same two species which Wiens and Scott (1975) calculated to cycle the greatest annual flow of trophic energy.

The four representative bird assemblages illustrate a diverse spectrum of feeding types (Table 7.1). Shallow-probing and surface searching-shorebirds, as the assemblage implies, are principally (71%) obligate benthivores which feed on benthic infauna and epibenthic zooplankton along the channel margin; the other species are omnivores whose diet includes vascular plant matter (including seeds) from adjacent marsh or terrestrial habitats. Waders are either functional benthivores who prey on similar, though somewhat deeper, benthic organisms as the first assemblage or are carnivorous (obligate or functional piscivores) on fishes and motile epifaunal invertebrates which venture into shallow sublittoral areas of the habitat. Surface and diving waterbirds, the largest assemblage, includes seven feeding types, over a third of which are functional benthivores. Obligate and functional piscivores and omnivores each comprise 19% of the total number of species in the assemblage although omnivores usually utilize estuarine channels only for roosting. Obligate herbivores and obligate and functionl planktivores were represented by one species each. Among the nine representative aerial-searching birds, two-thirds are higher level carnivores, either piscivores or avivores, while two are obligate insectivores and one is an obligate planktivore.

Recent studies in the Columbia River and adjacent estuaries have provided the first data directly focused upon estuarine utilization by aquatic (Dunn et al. 1981) and marine mammals (Howerton et al. 1980; Beach et al. 1981) which includes channel-specific food habits information; previous investigations tended to be either semi-quantitative and not channel-specific (Smith and Mudd 1976b) or were oriented toward marine and neritic habitats (summarized by Simenstad et al. 1979a and subsequently by Everitt and Jeffries 1979; Everitt et al. 1980).

Among the five representative terrestrial and aquatic mammals (Table 8.1), three are obligate herbivores which obtain their plant foods in adjacent terrestrial and wetland habitats while two are epibenthic carnivores which venture into channel habitats to feed. Beaver feeding activity in the Columbia River occurred principally in Sitka spruce habitat during all seasons except winter, when activity in the Sitka willow habitat was higher (Dunn et al. 1981). Muskrat and nutria, on the other hand, forage principally in high marsh habitats (Section 8.2), where muskrat preferentially eat water parsnip (Sium suave), Lyngbye's sedge (Carex lyngbeyi), and soft-stem bulrush (Scirpus validus); and nutria feed on a broader spectrum of plants, including reed canarygrass (Phalaris arundinacea), cattail (Typha sp.), Lyngbye's sedge, tufted hairgrass (Deschampsia caespitosa), tall fescue (Festuca arundinacea), water parsnip, and soft-stem bulrush (Howerton et al. 1980; Dunn et al. 1981). While muskrat illustrated no major seasonal variation in their foraging behavior, nutria feeding (no. feeding sites hectare^{-1}) appeared to reach a maximum in the fall and minimum in the summer: The reed canarygrass/cattail habitat was the most common foraging habitat in the spring and summer, Lyngby's sedge/horsetail in the fall, and colonizing soft-stem bulrush during the winter. Raccoon, the only truly terrestrial mammal utilizing estuarine channels for food resources, prey principally upon molluscs (e.g., clams such as Corbicula manilensis and Anodonta sp.), motile epibenthic crustaceans (e.g., crayfish and crabs), and fishes (e.g., eulachon, sculpins such as Cottus sp., carp, and starry flounder) with secondary input from birds (particularly waterfowl) and plant (rosaceae) seeds and fruits (Dunn et al. 1981). River otter in the Columbia River estuary generally overlapped with raccoon in their prey composition (principally crayfish, carp, Cottus sp., sculpins, and starry flounder), reflected a diet generally similar to that reported by Hirschi (1978).

All four representative marine mammals are facultative carnivores, three focusing their foraging principally upon pelagic prey assemblages and one on epibenthic assemblages (Table 8.1). Northern sea lions follow baitfish (e.g., eulachon) and salmon (e.g., spring chinook) into estuaries such as the Columbia (Beach et al. 1981), feeding principally at night and probably also consuming other schooling or large pelagic fishes in channel habitats (Simenstad et al. 1979a). As with the northern sea lion, no quantitative data on estuarine prey of California sea lions is available for this region, but it would be reasonable to assume that other pelagic schooling fishes (e.g., Pacific herring, northern anchovy, Pacific sand lance) and large demersal species (Pacific tomcod, starry flounder) also constitute potential prey in estuarine channels.

In addition to the focused, intensive foraging on eulachon in the Columbia River, harbor seals there and in other estuaries of the region prey upon other pelagic schooling and demersal fish assemblages and motile macroinvertebrates of channel and littoral flat habitats (Scheffer and Sperry 1931; Scheffer and Slipp 1944; Fisher 1952; Simenstad et al. 1979a; Brown 1980; Everitt et al. 1980; Beach et al. 1981; Bowlby 1981). Accordingly, principal prey species will include eulachon, northern anchovy, whitebait smelt, Pacific sand lance, longfin smelt, and Pacific herring among the schooling pelagic fishes; Pacific tomcod, Pacific staghorn sculpin, snake prickleback, English sole, starry flounder, shiner perch, lingcod, and bay goby among the demersal fish assemblage; and crangonid shrimp and Dungeness crab among the motile macroinvertebrates. Other prey which have been reported as prominent in harbor seal diet spectra, including Pacific hake (*Merluccius productus*), walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), various species of rockfish (*Sebastes* spp.), rex (*Glyptocephalus zachirus*), petrale (*Eopsetta jordani*), and Dover soles (*Microstomus pacificus*), are probably captured in non-estuarne habitats or in the outer margin of the estuaries' euhaline regions. Considerable inter-estuary and seasonal variation in diet composition also persists. Beach et al.'s (1981) analysis of harbor seal scat collected between June 1980 and April 1981 in the three major coastal estuaries of Washington indicates significant rank importance (based on frequency of occurrence) differences. For example, Pacific cod (20%), unidentified crustaceans (18%, probably crangonid shrimp and Dungeness crab), Pacific staghorn sculpin (16%), longfin smelt (15%), northern anchovy (14%), eulachon (13%), and snake prickleback (10%) were important in the Columbia River estuary; northern anchovy (21%), Pacific staghorn sculpin (19%), unidentified crustaceans (15%), shiner perch (13%), Dungeness crab (12%), and starry flounder (10%) dominated the prey spectrum in Willapa Bay; and northern anchovy (49%), Pacific staghorn sculpin (34%), English sole (23%), Pacific tomcod (17%), Dungeness crab (15%), and starry flounder (11%) predominated in Grays Harbor. Unequal monthly and total sample sizes and the inherent biases of frequency of occurrence data should be taken into account in evaluating these differences but the structural variability, as well as the commonality, in food web linkages between harbor seals and the variable secondary consumer levels in the three estuaries is apparent.

Seasonal diet variability is also obvious. Beach et al. (1981) also described seal foraging in the Columbia River estuary as shifting markedly from eulachon in the winter, to lampreys (class Agnatha, principally *Lampetra* spp.) in early spring, motile macroinvertebrates (crustacea) in late spring, and a diverse, opportunistic selection of fishes from summer to winter months. Seasonal shifts in Willapa Bay harbor seal diets were relatively different, from crustaceans in winter, to northern anchovy from spring through late summer, and a broader spectrum of fish species (led by Pacific staghorn sculpin and northern anchovy) from summer through fall. Likewise, Grays Harbor seals maintained a relatively different seasonal diet pattern: from Pacfic staghorn sculpins, pleuronectids, Pacific tomcod, and crangonid shrimp in the winter, to a diverse array of fish and Dungeness crab in the summer, to an emphasis upon northern anchovy in late summer, to Pacific staghorn sculpin and English sole in the fall.

In addition to these natural prey items, harbor seals, in conjunction with California sea lions, are also considered to be the principal cause of marine mammal damage to fishing gear but appear to be almost solely responsible for damage to net-captured fish, which accounts for as high as 7% of the sampled catch (Beach et al. 1981).

Although there are not data on harbor seal diet specific to estuarine channel habitats within the Straits of Juan de Fuca and Georgia and Puget Sound, information documented from this region (Scheffer and Sperry 1931; Fisher 1952; Calambokidis et al. 1978; Simenstad et al. 1979a; Everitt et al. 1980) indicates considerable overlap in prey taxa, indicating that estuarine channel fauna constitute a major element of harbor seal food resource in inland waters. Only fragmentary data is available on their food habits and little originates from this region; prey are assumed to be principally demersal fish, and pelagic fish and cephalopods (Simenstad et al. 1979a; Antonelis and Fiscus 1980; Everitt et al. 1980).

Integration of these food web relationships results in a composite food web for estuarine channel communities (Fig. 9.1) which is at least qualitatively oriented more toward detritus utilization and heterotrophic production than toward pelagic autotrophic production. If standing stock of detritivores and their predators is indicative, the food webs are qualitatively dominated by detrital carbon. As identified by de Sylva (1975), Odum and Heald (1975), and Northcote et al. (1979), most estuarine food webs fall into two categories: 1) relatively clear, deep systems where organic carbon is derived primarily from phytoplankton production, and 2) comparatively turbid, shallow estuaries where the carbon originates from a combination of macrophytic production (both exogenous and endogenous), which is degraded to detritus and utilized by microflora, and periphyte production. Very few estuaries in the Pacific Northwest fall into the first category, especially if we include those estuaries which, although seldom turbid, may have food webs based upon dynamic, short-term recycling of endogenous carbon exuded by angiosperms, macroalgae, and epiphytes (Wissmar and Simenstad, Fish. Res. Inst., Univ. Wash., unpubl. data; see Section 4.1). Thus, direct (pelagic) autotrophic production is only marginally supportive of estuarine food webs in the region and is generally restricted to the large coastal estuaries where freshwater and esturine phytoplankters are entrained in a confined euphotic zone.

Among these generalized food web linkages are several distinct modules (Paine 1980) which typify estuarine channel communities, not only in structure but often in common consumer taxa. The shortest, least-compartmented food web (it is still a "web" due to considerable predator-prey interaction within a compartment such as the benthic infauna) is that Northcote et al. (1979) described as:

detritus⇨benthos⇨benthophagous fishes

when tertiary consumers included, the archetypical food webs in this category would include both "detritus:benthic infauna:obligate benthivore:functional epibenthic carnivore" modules as well as "detritus:epibenthic zooplankton:functional epibenthic planktivores:functional epibenthic carnivore" modules such as:

More complexity is evident in detritus-based, epibenthic modules which involve

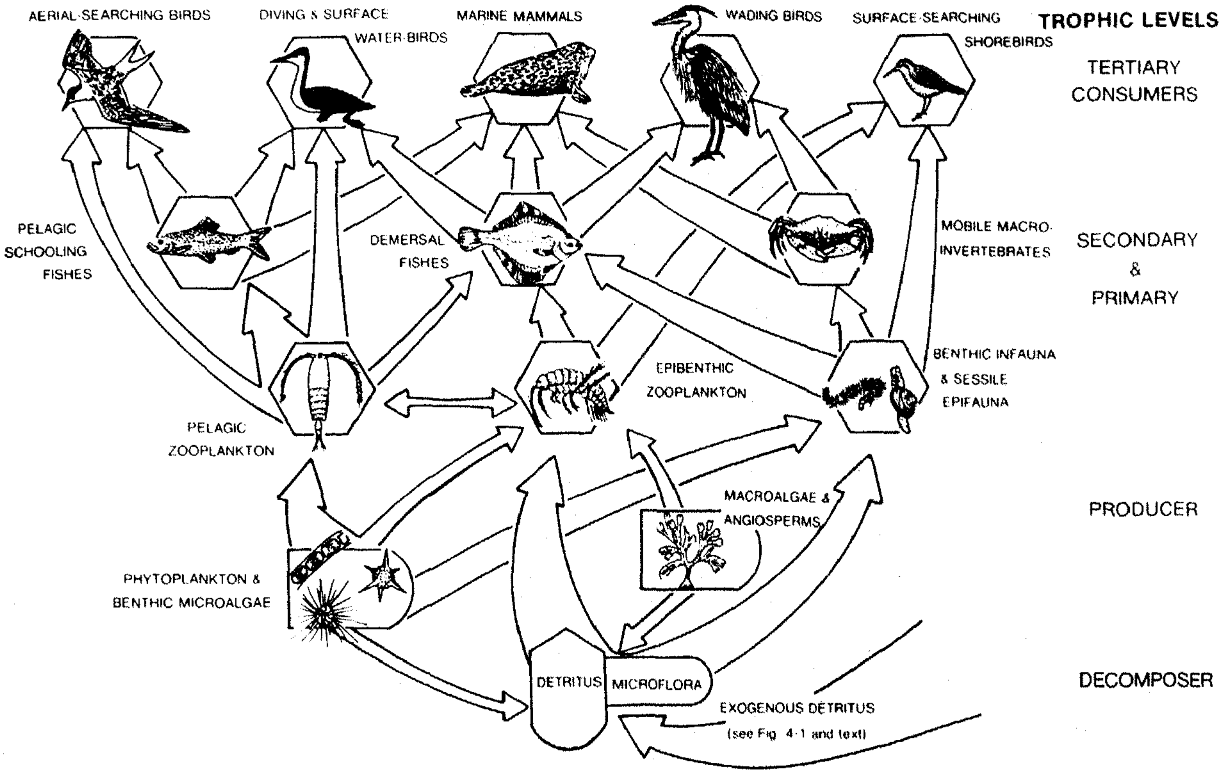
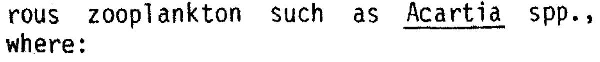


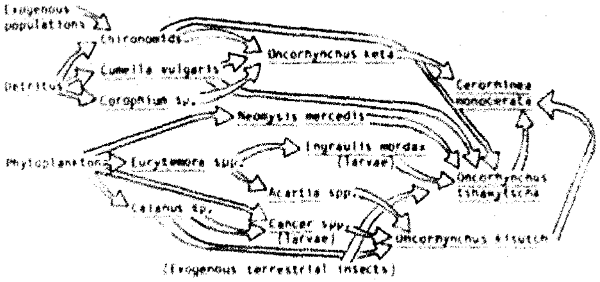
Fig. 9.1. Representative food web of estuarine channel habitats of the Pacific Northwest; sizes of linkage arrows illustrate relative biomass transfer.

meiofauna carnivores such as Crangon spp. or benthic carnivores such as Cancer spp., resulting in "detritus:detritivorous epibenthic zooplankton:benthic/epibenthic carnivore (2°):facultative epibenthic carnivore (3°)" modules such as:



Planktonic food webs are characteristically shorter, as represented by the phytoplankton:herbivorous pelagic zooplankton:obligate planktivore: obligate piscivore module, although they can be complicated by the inclusion of carnivorous zooplankton such as Acartia spp., where:

The ultimate complexity is represented by modules including species which are either extremely plastic (facultative) in the feeding behavior or incorporate or grow through several feeding strategies over the period of residence in the estuary. This is particularly evident in the case of juvenile salmonids, which utilize both endogenous and exogenous (to the habitat and, often the estuary) detritivores and herbivores. The resulting modules can be ambiguously described as detritus/phytoplankton: detritivorous epibenthic zooplankton/ herbivorous pelagic zooplankton:epibenthic carnivore:facultative epibenthic/pelagic planktivore:obligate piscivore such as shown on the following page. Of course, this complexity seldom exists to this extent within any channel class, order, or configuration, or any size class of consumer (e.g., juvenile salmonid) at any one time, but varies uniquely as a function of all these variables.



Classically, the diversity (i.e., number of connections or "connectence") and strength of these interactions have been correlated with the stability (i.e., its inherent susceptibility to collapse to a different, usually less diverse structure when perturbed by removal of linkages or nodes); this poses the question of whether food webs are "structured" or "unstructured" (MacArthur 1955; Watt 1964; Paine 1966, 1969; Gardner and Ashby 1970; Isaacs 1972, 1973; May 1972, 1973; De Angelis 1975). The implications of mutalistic relationships have also been recently incorporated into these models (Vance 1978). Unfortunately, the functional resilience of these modules, their linkages, and their dependence upon external events has seldom been investigated from the standpoint of the processes generating their structure and, until that resolution of research is applied to estuarine channel communities, the question of food web stability will remain unresolved. We can, however, selectively examine exemplars of prominent predator-prey or competition interactions for clues to the strength of linkages within representative modules or of the potential stability of the simpler modules *in toto*.

9.2 ROLES OF PREDATION AND COMPETITION INTERACTIONS IN STRUCTURING COMMUNITIES AND FOOD WEBS

There are, among the modules described in the previous section, illustrations of strong predator-prey and competition interactions wherein the distribution and abundance of estuarine channel organisms, and thus the structure of the community, are contingent upon the presence and magnitude of these linkages. Although few of these examples originate from Pacific Northwest estuaries, they are sufficiently close analogues that reasonable inferences to the region's estuarine channel communities might be made.

One of the strongest linkages suggested is that between the calanoid *Acartia* spp. which could represent an important predator upon the larvae of the dominant estuarine calanoid in the region, *Eurytemora* spp. Hodgkin and Rippingale's (1971) interpretation of Cronin et al. (1962), and Jeffries (1967) accounts of zooplankton in North American estuaries indicated that *Acartia*, by its carnivory upon critical life history stages of the estuaries' *Eurytemora* populations, may prevent significant recruitment to the adult population. Comparable *Acartia*/*Eurytemora* data sets also exist for Yaquina Bay (Frolander et al. 1973), the Columbia River estuary (Haertel and Osterberg 1967), Netarts Bay (Zimmerman 1972), and Grays Harbor (Simenstad and Eggers 1981). Further testing and verification of this hypothesis must depend upon further detailed analysis of these datasets.

The potential for predation structuring of epibenthic harpacticoid copepod assemblages in shallow sublittoral habitats of Hood Canal by juvenile chum salmon was suggested by Simenstad et al. (1980) and Simenstad and Salo (1982). Given the intensive, selective foraging pressure that juvenile salmonids exert upon epibenthic harpacticoid copepod (e.g., *Harpacticus*), gammarid amphipod (e.g., *Corophium*), and cumacean (e.g., *Cumella*) taxa, it is highly probable that prolonged foraging upon these epibenthic prey resources by high densities of juvenile salmon could result in dramatic restructuring of that assemblage. This is even more probable given the high density, pulse releases of juvenile salmon from hatcheries which may result in millions of fish entering estuaries at one time.

Although there has been no comprehensive, estuary-wide examination of such a relationship, the same situation may exist in the pelagic environs of those estuaries which experience high densities of larval and juvenile planktivorous fish. Yaquina Bay, the Columbia River estuary, and Grays Harbor have well-documented concentrations of Pacific herring, northern anchovy, and smelts (particularly surf and longfin) which are both temporally and spatially abundant during certain seasons (see Section 6.2). But Johnson's (1981) analysis of the *Acartia californiensis* population in Yaquina Bay (see Section 5.4) provides ample evidence that such selective predation can effectively control abundance cycles, and ultimately production, of the prominent members of these zooplankton assemblages. Under such intense and selective foraging pressure on pelagic zooplankton, predominantly these calanoid copepod taxa, these obligate planktivores may well structure the composition, diversity, and standing stock of the estuarine channel zooplankton assemblage.

Sitts and Knight (1979) and others (C. Simenstad, Fish. Res. Inst., Univ. Wash., unpubl. data) have produced evidence that the crangonid shrimp *Crangon franciscorum* often feeds extensively upon the mysid *Neomysis mercedis*. Sitts and Knight in fact, estimated that *C. franciscorum* removed between 0.1% and 5.0% of the *N. mercedis* biomass daily from the Sacramento-San Joaquin River estuary, and that, by preying selectively upon intermediate sized (4-7 mm) mysids, the shrimp are significantly affecting the mysid population structure. The persistence of such a *Crangon*-*Neomysis* interaction in the Pacific Northwest, particularly in the large coastal estuaries which maintain large populations of both taxa, is highly probable and further illustrates the importance of the detritus-based module involving the epibenthic zooplankton prey of mysids (*N. mercedis*) and shrimp (*C. franciscorum*), and the prominent predators on the shrimp (starry flounder and harbor seal). The relative importance of this particular module may be evaluated in final synthesis of the CREDDP studies (Col. Riv. Est. Study Team, pers. comm.), which included quantitative assessment of these taxa in the Columbia River estuary in 1980-1981.

9.3 ESTUARINE CHANNELS AS CRITICAL REPRODUCTIVE, NURSERY, FORAGING, AND REFUGIA HABITATS

Establishment of utilization patterns and food web modules involving estuarine organisms carries implicit assumptions of dependence upon these relationships most of which, however, are completely unverifiable. Whether the loss or major disruption of a food web linkage or microhabitat would actually result in the subsequent decline in the population remains conjecture unless controlled manipulation experiments can be conducted. But, unlike those which have been successfully conducted in marine rocky littoral (see Paine 1977, among many) and shallow sublittoral sand- or mudflat habitats (Virnstein 1977; and Woodin 1981; among not so many; but see Hurlberg and Oliver 1980 for discussion of interpretive limitations), effective manipulations within the dynamic estuarine channel habitats have seldom been attempted and would be even more difficult to interpret due to extreme variation in uncontrollable physiochemical conditions. The following illustrations of potentially "critical" habitat associations are, therefore, only descriptive hypotheses which remain to be effectively tested.

Compared with other habitats, estuarine channels appear to be limited in providing optimum conditions for reproduction of most fauna. Except in the case of blind (e.g., tidal) channels, high water velocities and unstable bottom sediments in most channel habitats inhibit many invertebrates and vertebrates from establishing nesting sites; even the suitability of the tidal channels is often limited by tidal dewatering. Fauna which do spawn in channels typically deposit adhesive eggs (gastropods, lingcod), bury their eggs (salmon), or carry and brood the eggs and larvae/juveniles (gammarid amphipods, i.e., *Eogammarus* spp.; Dungeness crab). But, except for the spawning immigration of salmon (typically chum and pink salmon) into the channels of estuaries' upper reaches, most reproductive activities are confined to resident fauna which undergo their entire life cycle within the estuary. Many estuarine residents, however, emigrate from channel to other habitats to reproduce. Estuarine birds, of course, are the extreme case, as none actually nest within the habitat. But resident fishes such as sturgeons, smelts, gobies, stickelbacks, and many sculpins move to either channel boundaries or other esturine habitats (e.g., shallow sublittoral or littoral sand- or mudflats; saltmarshes) to spawn.

Whether from resident or exogenous populations, both invertebrate and vertebrate larvae and juveniles can reside within estuarine channels for extended periods of time, essentially utilizing the habitat as a "nursery" until settling out into benthic, epibenthic, or demersal assemblages or moving out of the habitat. The net outlfow circulation pattern of the estuaries, however, represents a major inhibitor to prolonged entrainment of planktonic larvae. Assuming neutral buoyancy and passive behavior, the minimum rate of reproduction required for an endemic zooplankton population to maintain itself in an estuary is determined by the rate of circulation, such that reproduction must be higher than the tidal exchange loss rate (Ketchum 1951, 1954). But the organisms' behavior is not passive and particular life history patterns and behaviors of such organisms have evolved to optimize their estuarine residence time. Carriker (1951), Bousfield (1955), Pearcy (1962), Wood and Hargis (1971), Graham (1972), de Wolff (1974), Sandifer (1975), Wheeler and Epifanio (1978), Cronin and Forward (1979), and Cronin (1982) have all described behavioral retention mechanisms exhibited by larvae in two-layered estuaries having net landward flow along the bottom during periods when larvae are abundant. Their studies illustrated that larvae can prolong their residence in the estuary by actively migrating into the landward-flowing surface water on flood tides. Similar retention mechanisms have also been postulated to account for the maintenance of resident zooplankton (e.g., Eurytemora) populations in estuaries (Rogers 1940; Hurlbert 1957; Wooldridge and Erasmus 1980). Carriker (1959), Sandifer (1975), and Johnson and Gonor (1982), however, have illustrated situations where some estuarine larvae are flushed out of the estuary of origin, only to be transported back into other, adjacent estuaries as later larvae, post-larvae, or juveniles. Johnson and Gonor (1982), in fact, estimated that 88% of the total abundance of Callianassa californiensis stage I zoea were carried out of the Salmon River estuary on the ebbing tide; this would result in a "leap-frog" transport and metamorphosis of larvae in and out of estuaries along the coast until they settled out in the benthic form. Johnson and Gonor (1982) suggested that the concentration of Callianassa larvae in the coastal neritic waters and successful recruitment to coastal estuaries was enhanced by the alternation of active upwelling and relaxation periods which Huyer (1976) described off Oregon. Thus, the extent and importance of estuarine retention of larvae may depend upon both the position of the reproducing population, since maximum retention will occur with populations in the upper reaches of the estuary (Dayton and Oliver 1980), as well as the evolved behavioral repertoire and seasonal periodicity of the reproductive and early life history events.

Pearcy and Myers (1974) provide one of the few comprehensive assessments of the value of a Pacific Northwest estuary as a nursery habitat for larval fishes, excluding McHugh's (1967) suggestion that Pacific coast estuaries are less important than eastern seaboard estuaries. They established that, indeed, larvae of most species were more common offshore than within the estuary and that Pacific herring larvae were the only commercially-important species to utilize the estuary as a nursery habitat. Other, less notorious species which were also identified to utilize Yaquina Bay were bay goby, prickly sculpin, buffalo sculpin, and Pacific staghorn sculpin (see Table 6.2); other studies also suggested that postlarval and juvenile embiotocids (P. furcatus, R. vacca, and E. lateralis) also are prominent (Beardsley 1969; Wares 1971). Later studies of the zoo- and ichthyoplankton of the Columbia River and

Grays Harbor estuaries suggest that larval and juvenile northern anchovy, surf and longfin smelt, and eulachon should also be considered as nursery residents in the coastal estuaries (see Sections 6.2.1-6.2.3.).

Although their larvae are not often documented as abundant components of the ichthyoplankton, juvenile pleuronectids (prominently starry flounder, English sole, and speckled and Pacific sanddab) are abundant in demersal fish assemblages, particularly those which occupy shallow sublittoral regions of estuarine channel and adjacent tideflat habitats (Westrheim 1955; Beardsley 1969; Olsen and Pratt 1973; as well as those cited in Section 6.1). These species often illustrate increasingly deeper depth distributions relative to increasing fish size, such that they appear to move off the tideflats and further into the channels as they grow larger. This depth-size relationship has not been well-documented, nor have the causal mechanisms been evaluated, although both predator avoidance and foraging on optimal prey resources could explain this transition.

Juvenile salmonids illustrate one of the better example of active retention in estuarine channels over a critical period in their early life history. The five species show varying durations of estuarine residence (Table 6.3), with marked intraspecific variation resulting from respectively variable times and sizes at entry into the estuary. Within the estuary are a diverse array of prey resources, often in extremely high density (e.g., harpacticoid copepods, Corophium amphipods, chironomid larvae, decapod and fish larvae), which allow the juvenile salmon to sustain high growth rates (as high as 6% body weight per day) while occupying a relative refugia from predation (Simenstad et al. 1982b); whether through schooling in shallow sublittoral, eelgrass habitats (i.e., juvenile chum salmon) or turbid pelagic waters (i.e., chinook smolts), these systems may be narrowing the "window of vulnerability" to predation outside the estuary by "growing out" of it while in the estuary. This relationship between estuarine residence time and foraging success, and the implications to the total marine survival rate, suggests that the distribution and abundance of the principal preferred prey (Table 9.1) ultimately determine the production of the salmon populations migrating through the system (Northcote et al. 1979; Simenstad and Salo 1982; Simenstad et al. 1982a, b).

9.4 INTERRELATIONSHIPS AMONG ESTUARINE CHANNEL HABITATS AND RIVERINE, WETLAND, OCEANIC, AND OTHER ESTUARINE HABITATS

Food web and other ecological interactions among channel and other estuarine habitats as well as with habitats outside the estuary are manifold. They range from simple transport of pelagic phytoplankton and zooplankton into and out of the channel community from and to riverine and oceanic sources, to the complex exchange and entrainment of exogenous detritus. These, like the transport of larval fish and invertebrates into the habitat, are relatively passive actions which result from physical (e.g., tidal) influences. Other transfers, such as the migrations of anadromous fishes and birds, can occur on a seasonal scale, whereas the movement of fishes from the shallow sublittoral flat habitats into the channel habitats with tidal dewatering occur approximately every six hours, involve active movements of organisms but may be equally predictable.

At the base of the estuarine channel food web, detritus constitutes the most critical material originating from outside the community. Alteration of the detritus resource--its supply, timing, or character--to estuarine channels poses direct impacts upon the structure and standing stock of all consumer organisms in those food web modules based upon detritivores. Whether originating from riverine sources completely outside the estuary (e.g., DOC; Naiman and Sibert 1978) or from within adjacent habitats (vascular saltmarsh plants; Kistritz and Yesaki 1979), the accumulation and retention of detritus is dependent upon the complex factors effecting circulation and salinity intrusion. The endogenous sources of trophic energy, autotrophic producers such as phytoplankton and algae, do not, on the other hand, provide an equivalent proportion of the total carbon budget cycling through the community.

Primary consumers are typically endemic populations. Benthic infauna and sessile epifauna are obviously resident assemblages but the organisms recruiting to these populations originate from parent assemblages outside that particular estuary, perhaps even from other, adjacent estuaries (see Section 9.3). Extreme examples of primary consumers (or prey resources of secondary consumers such as juvenile salmonids) which originate from outside the community are the terrestrial insects which are transported into the neuston assemblage from the watershed upriver or are blown in from wetland and upland habitats bordering the estuary.

More motile secondary and tertiary consumers include progressively more nonendemic populations, which either derive their recruitment from outside the community (e.g., Pacific herring, northern anchovy) or intermittently occupy the habitat for important functions (e.g., foraging by harbor seals; roosting by migratory seabirds). Accordingly, many of these immigrants are critical components of prominent food web modules and through these roles are largely responsible for the structure of their prey assemblages.

The community also exports considerable biomass, both passively through the net flow out of the system, carrying varying proportions of the pelagic phytoplankton and zooplankton to oceanic habitats, and actively through the emmigration of secondary and tertiary consumers. The end result of the nursery process involving larval and juvenile fishes discussed earlier provides the best example of this export: almost all baitfish--herring, smelts, anchovies, eulachon--which reside in estuarine channels during their early life history eventually migrate out of the estuary after consuming a large portion of several year's pelagic zooplankton production.

CHAPTER 10

SUMMARY - THE ROLE OF CHANNEL HABITATS IN ESTUARINE ECOSYSTEMS AND MANAGEMENT IMPLICATIONS

In essence, the role of channel habitats can metaphorically be equated to that of any living organism's circulatory system in that transport of energy, nutrients, wastes, and the living products of an estuarine ecosystem flow within these passages. Similarly, as the loss of peripheral appendages or organs may not necessarily affect the ultimate function of circulation, loss of adjacent estuarine habitats may not depreciate this transport role of channels; however, the carrying capacity and production of the overall system (i.e., it's quality) will undoubtedly decline. On the other hand, significant inhibition of channel habitats' capacities to function, like arteriosclerosis, will ultimately result in deterioration of the whole estuary as a healthy, productive ecosystem. It is difficult to understand, then, why channels have typically been some of the most highly impacted habitats but typically the most ignored estuarine environs when management goals and priorities are set. Presumably, the dynamics of continuous riverine and marine infusion of high quality water and organisms are assumed to naturally mediate the insults occurring within the estuary itself or those interjected into the system from upriver or from the ocean. But, as a result, several estuaries in the Pacific Northwest have become burdened with supposedly innocuous modifications to the point of disfunction.

Of all estuarine habitats, channels have undoubtedly been diminished quantitatively the least. Bortleson et al. (1980) have illustrated some of the dramatic losses of subaerial wetland habitat (100% in Puyallup River, 99.2% in Duwamish River, and 96.4% in Samish River estuaries) but indicated no losses in channel habitat. Thomas' (1982) exhaustive analysis of habitat changes in the Columbia River estuary since 1868 provided an estimate of 10.4 km^2 of deep water (>6 m below MLLW) habitat lost since that time. Over the entire estuary, this is a change of only 7.3%, as compared to losses as high as 76.8% for other habitats (i.e., tidal swamps). This relatively minor loss of habitat applies, however, only to mainstem and subsidiary channels. Losses of blind or tidal channel habitat are much more extensive but unfortunately unestimated. Thomas (1982) estimated a 43.2% loss (28.3 km^2) of tidal marshes in the Columbia River estuary and Levy (1980a) a 39% (0.23 km^2) loss of estuarine marshes in the Fraser River estuary, but it is impossible to estimate what portion of these losses involved channel habitats.

Qualitative changes in estuarine channels, however, have been rampant since "civilized" man arrived in the region. Some of these are the result of accretion and erosion unrelated to man's influence, but are symptomatic of the natural "aging" processes in the evolution of an estuary. In the more than 100 years since the Columbia River estuary was first mapped in entirety, this relatively undeveloped estuary has undergone some dramatic changes in channel configuration (Fig. 10.1). Certainly changes over the last forty years can be attributed partially to anthropogenetic alterations such as dredging and dredge spoil disposal within the estuary and hydroelectric power dam construction (and resulting river discharge alteration) outside the estuary. But it must be remembered that these processes are characteristic of the normal physical dynamics of an estuary and, although they can be modified by man's

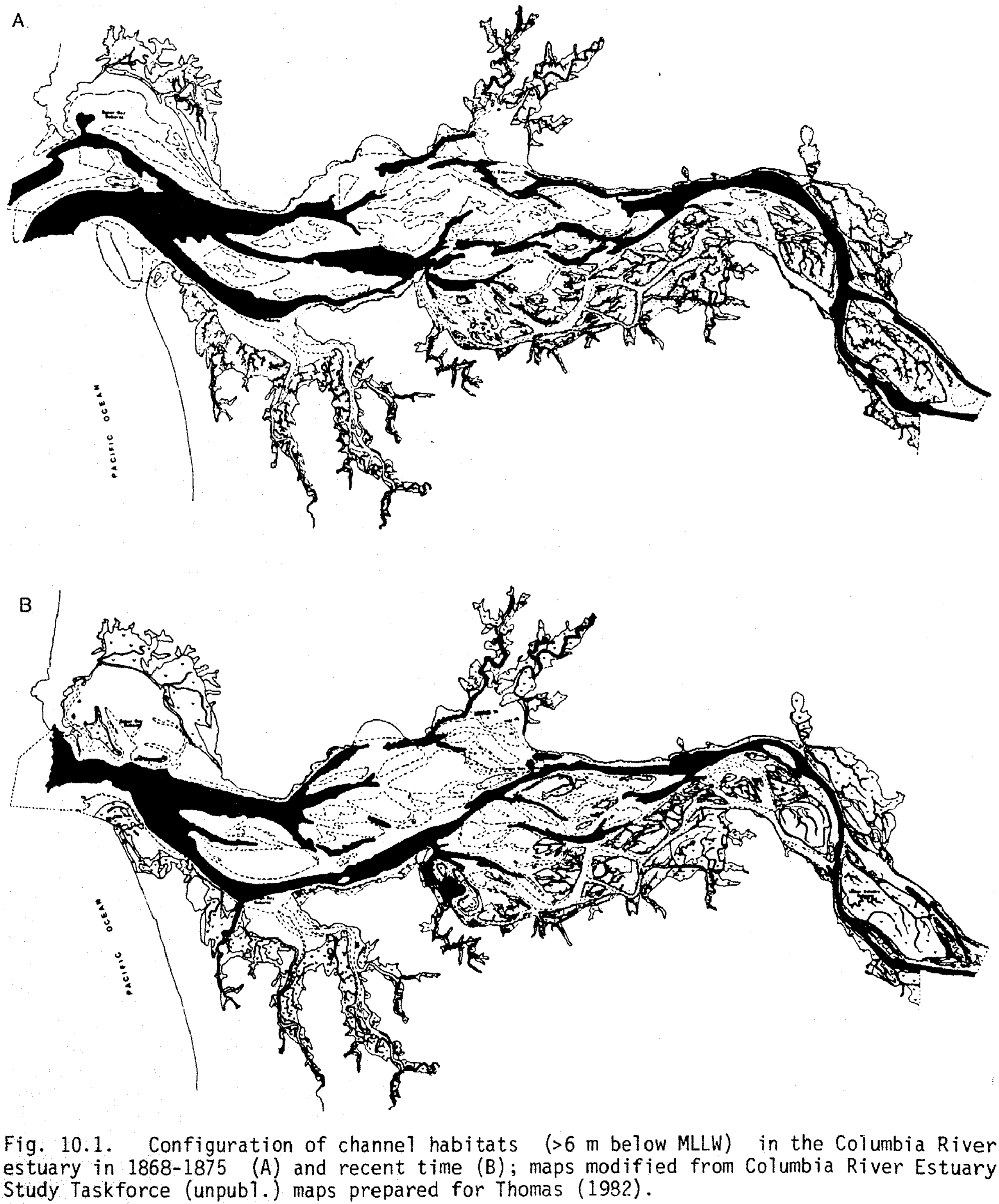


Fig. 10.1. Configuration of channel habitats (>6 m below MLLW) in the Columbia River estuary in 1868-1875 (A) and recent time (B); maps modified from Columbia River Estuary Study Taskforce (unpubl.) maps prepared for Thomas (1982).

structures and other manipulations are seldom eliminated. For example, during the last 100 years the volume of the Mersey River, England, estuary has declined about 10% despite dredging of over 500 x $10^6 m^3$ of material (Price and Kendrick 1963).

Physiochemical attributes such as salinity and their influence upon the estuary's communities have also been altered over time as a result of the effect of bathemetry upon estuarine mixing and salinity intrusion. Thomas (1982) theorized that more extreme flow fluctuations, extensive shoaling, and a measurably different geomorphology of the entrance to the Columbia River estuary formerly produced more temporally and spatially extreme salinity regimes than now exist. The result was probably an essentially freshwater system at all stages of tide during large spring freshets and increased salinity intrusion during periods of low discharge; this may have been substantiated by the reports of significantly brackish water near Gray's Point in 1805 (Thwaites 1959); see Fig. 10.1.

Qualitative change in estuarine channel morphology has also changed the demography of man's exploitation of estuarine fish fauna. This is best illustrated by the changes in commercial salmon fishing strategies in the Columbia and Fraser Rivers estuaries, wherein dredged navigation channels can now be fished much more effectively by certain net (drift gillnet, purse seine) fisheries.

So man's influence is superimposed upon a naturally evolving, dynamic system. The difference is in the short-term, intense perturbations man continues to impose upon estuaries.

10.1 SOURCES AND MECHANISMS OF IMPACT

A suite of impacts result from man's development of estuaries and their contributing watersheds. Among the major perturbations occurring within the channel which can produce deleterious impacts to the estuarine ecosystem are:

1) Dredging and dredge-spoil disposal;
2) Filling and other so-called land reclamation;
3) Jetty, training wall, and other construction;
4) Urban and industrial effluent discharge;
5) Log dumping and storage;
6) Commercial or recreational exploitation of fauna and its artificial enhancement; and
7) Upstream water diversions and storage reservoirs.

In addition to these, alterations to adjacent estuarine or exogenous riverine or upland habitats which indirectly insult estuarine channels include:

1) Logging;
2) Hydroelectric power development;
3) Agriculture; and
4) Mining.

Only the endogenous impacts will be discussed in this synthesis.

Dredging and dredge-spoil disposal has been probably the most extensive, and often the most blatant, modification imposed upon channel habitats (Fig. 10.2). Just the magnitude of sediment removal is astounding. In the Columbia River estuary alone, including the mouth and bar, over 4.6 x $10^6 m^3$ of bottom sediment is dredged annually (based on most recent 5-year data, L. Smith, U.S. Army Corps of Engineers, Portland, OR, pers. comm.) or over 25% of the estimated annual deposition (Gross 1972). Elsewhere along the coast, 1.6 x $10^6 m^3$ is dredged annually in Oregon estuaries, principally in Coos Bay, the Umpqua River estuary, Yaquina Bay, and Suislaw River estuary (Smith, pers. comm.); about 2.3 x $10^6 m^3$ is dredged annually in Washington State, over half of that in Grays Harbor (Simenstad et al. 1982b); and 0.4 x $10^6 m^3$ is dredged annually along the northern coast of California, almost entirely in Humboldt Bay (B. Dixon, U.S. Army Corps Engineers, San Francisco, CA, pers. comm.).

General literature on environmental effects of dredging is extensive (see

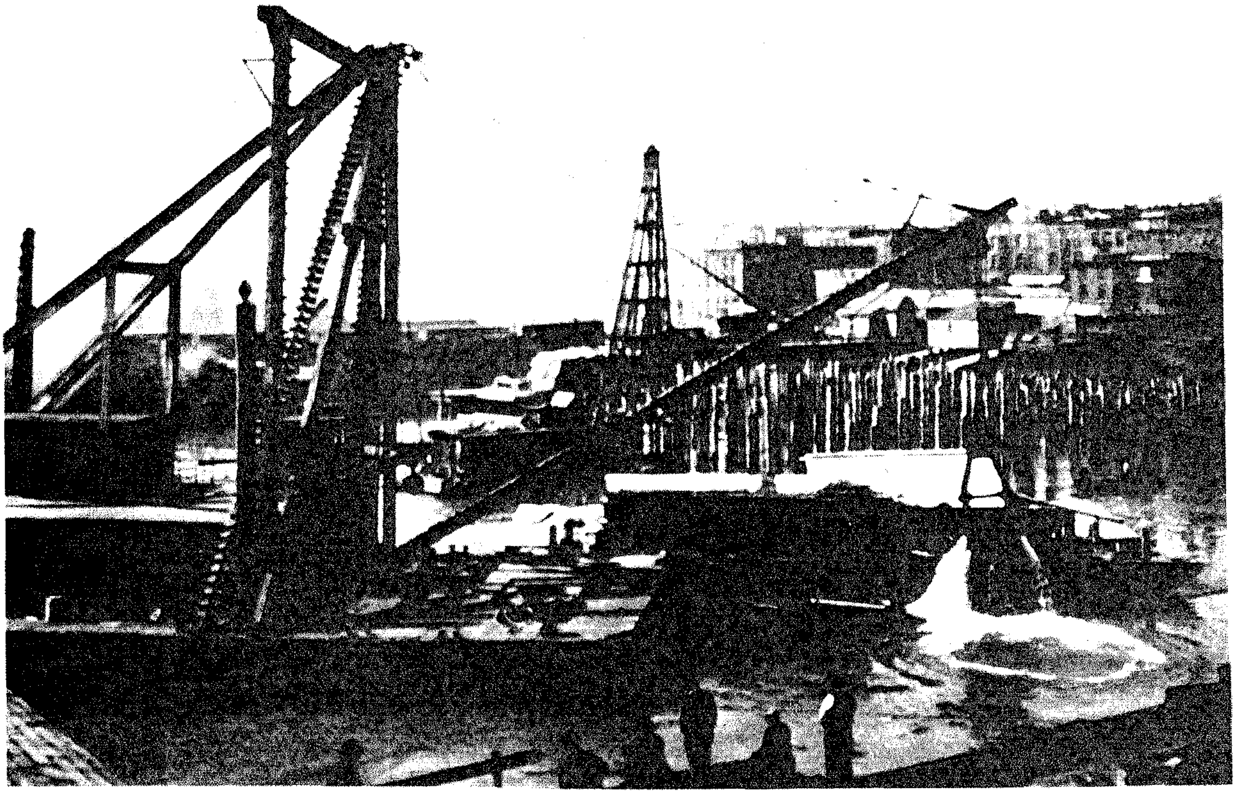


Fig. 10.2. Late 1800's dredging of Duwamish River channels and littoral flats in Elliott Bay, Seattle, Washington (photo by Ashel Curtis; reproduction courtesy of University of Washington Historical Photography Collection).

Natl. Tech. Info. Serv. 1981a, b, and c for recent citations), but empirical information from channel habitats in Pacific Northwest estuaries is very limited (O'Neal and Sceva 1971; Slotta et al. 1973; Jeanne and Pine 1975; Krenkel et al. 1976; McCauley et al. 1976; J.L. Smith et al. 1976; J.M. Smith et al. 1976; Blazevich et al. 1977; McCauley et al. 1977; Oregon State Univ. 1977; Stephens et al. 1977; Bella and Williamson 1979-1980). Due to the complex nature of dredging and its influences upon estuarine environs, a comprehensive discussion of dredging effects is beyond the scope of this synthesis although there is a dramatic need for such a document.

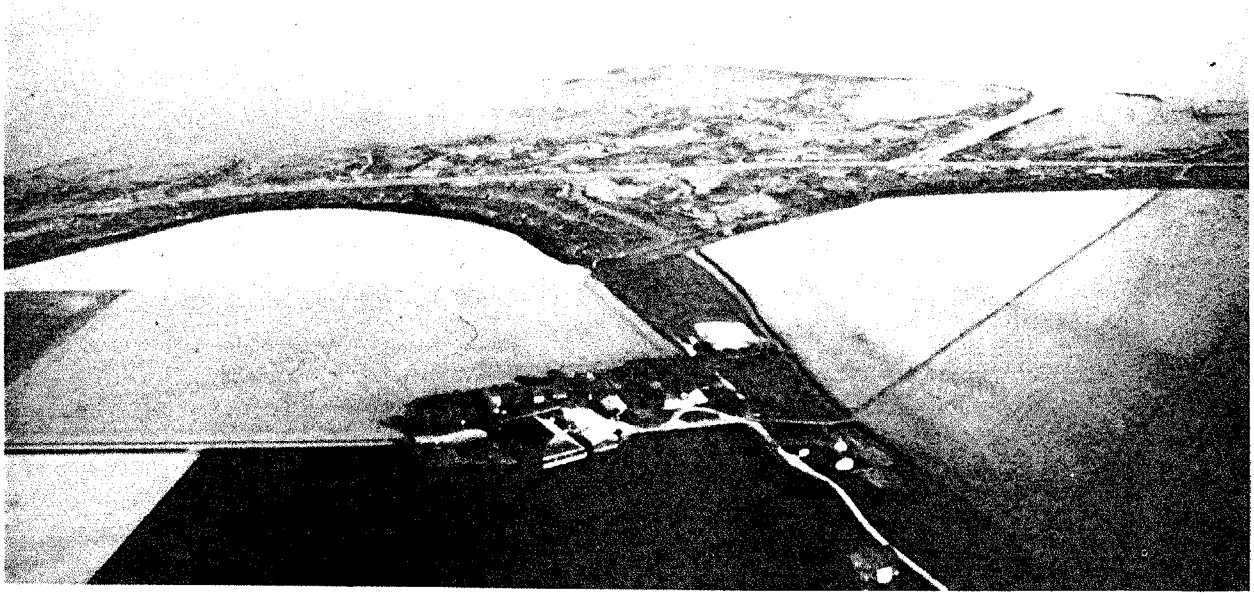
In general, deleterious effects of dredging activities result from a variety of direct and indirect mechanisms. Acute reductions in organism or community standing stock can occur through: 1) mortality induced by uptake through the dredge; 2) removal of benthic habitat; 3) burial by dredge spoils or through resettlement of suspended sediments adjacent to dredging site; 4) release of toxic substances from dredged sediments into pelagic or benthic habitats; and 5) organic enrichment causing excessive biological oxygen demand. Impacts will not necessarily be long-term if cessation or removal of these perturbations is prompt and thorough. Indirect effects can also result in eventual degradation of the biological community, although they are usually manifested over longer time periods and are more effective upon community structure due to species-specific interactions. These effects include: 1) sublethal decline in water quality (e.g., dissolved oxygen, turbidity, nutrients, heavy metals, pesticides) or sediment quality (e.g., particle size distribution, % volatile solids, depth distribution and magnitude of redox potential, heavy metals); and 2) modification of current patterns and salinity intrusion as a result of changes in estuarine bathymetry.

Evaluation of behavioral responses of aquatic organisms to dredging and the implications to their ultimate survival has seldom been attempted, however. Even in the absence of any sublethal effects to dredge-suspended sediment (i.e., Kehoe 1982), organisms such as juvenile Pacific salmon, which depend upon channel habitats as migration corridors, may actively avoid certain turbidity levels (Bisson and Bilby 1982) to the detriment of their ability to feed effectively or to avoid predators.

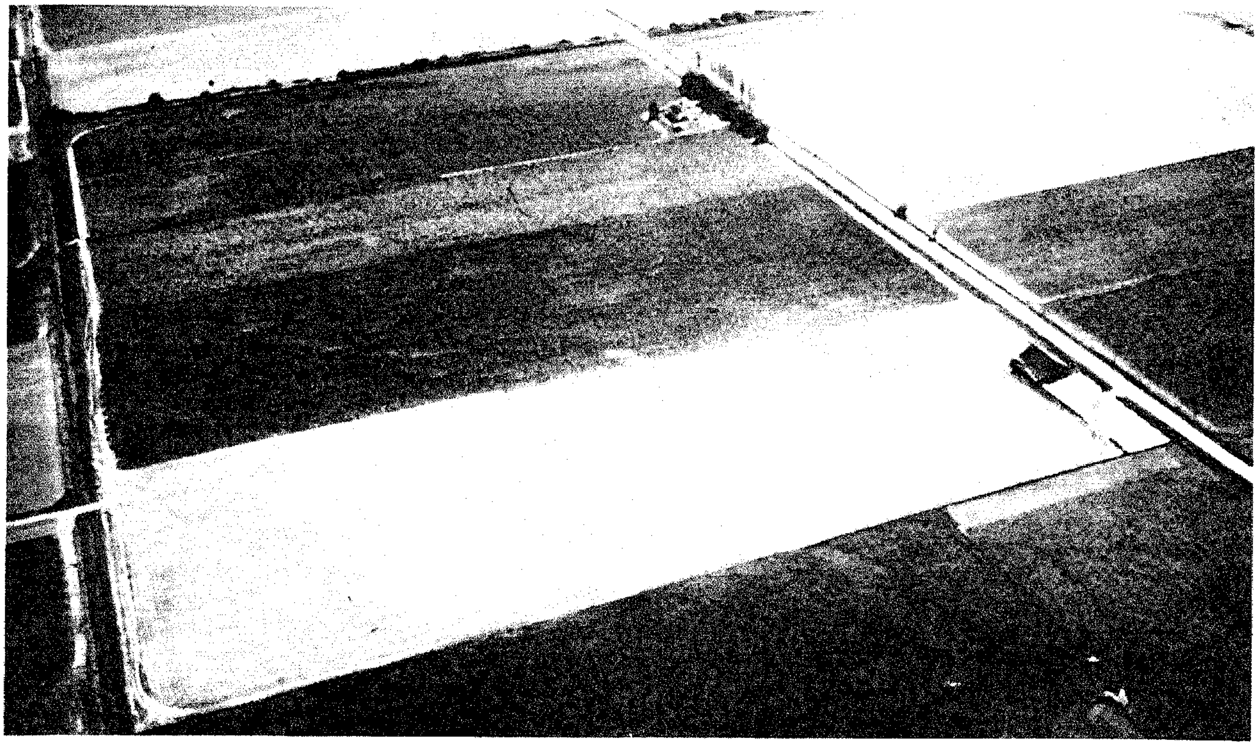
Filling and diking have obvious direct effects by removal of blind (tidal) channels which characterize tidal marsh and swamp habitats. This has been a pervasive modification of many Pacific Northwest estuaries (Fig. 10.3) and, given the apparent dependence upon these shallow channel systems by certain juvenile salmonids (see Section 6.2; Levy et al. 1979; Anderson et al. 1981; Levy and Northcote 1981; Congleton et al. 1982; Levy and Northcote 1982; Levy et al. 1982), the removal of such optimal habitats may be a major contributor to the decline of many native salmon runs throughout the region.

In addition to the direct elimination of channel habitat, the construction of structures such as dikes, jetties, and training walls in or adjacent to channels often impose far-reaching effects upon estuarine circulation. Current velocities and salinity intrusion are commonly altered as a result of flow constriction or inhibition, resulting in direct modification of the behavior of organisms and communities limited to specific current velocity and salinity regimes or indirect impact by loss of food resources or refugia. Levings and Chang (1977) compared current velocities in a "back channel" (Williamson Slough; 60 cm sec^{-1}), within influence of a wing dam (Steveston Island; 75 cm sec^{-1}), in mid-channel (Ladner Reach; 90 cm sec^{-1}), and adjacent to a training wall (Woodward; 104 cm sec^{-1}) in the Fraser River estuary and found significant differences due to the influence of the training wall although not of the wing dam. Interpretation of Brett's (1970) and Brett and Glass' (1973) response surfaces for critical swimming speed of juvenile sockeye salmon would suggest that feeding activities under temperatures expected during estuarine outmigration involve sustained swimming speeds of under three lengths sec^{-1}. Extrapolating their relationships to the expected lengths of other outmigrating salmon species, it would appear that normal feeding behavior would be disrupted at water velocities greater than 40 cm sec^{-1}. Levings and Chang (1977) also suggested that important prey of juvenile salmon, such as the gammarid amphipod Eogammarus confervicolus, would have difficulty even remaining on the bottom or attached to algae at current velocities greater than 10 cm sec-1; Levings (1973) found that much higher, sustained velocities ($\sim$250 cm sec^{-1}) would actually flush A. conferivicolus out of the inner Squamish River estuary. This illustrates what may be an element of the functional relationships between water velocities, prey availability, and foraging behavior of juvenile salmon. The fact that juvenile salmon do, indeed, feed predominantly in subsidiary and blind channels where the highest standing stock of benthic, epibenthic, and drift prey are found, illustrates the potential deleterious effect of increasing channel water velocities in these habitats.

Modification of current velocities along the bottom and the resulting restructuring of bottom sediments can also lead to shifts in trophic associations of benthic infauna. Wildish (1977) and



A



B

Fig. 10.3. Example of where diking and filling have removed (blind or tidal) channel habitat in Fraser River estuary; (A) illustrates diking of subsidiary (entering from lower right) channel and blind channels in saltmarsh, and (B) shows historical channel patterns still evident in existing fields (photos courtesy of David Levy, Westwater Research Centre, University of British Columbia, Canada).

Wildish and Kristmanson (1979) hypothesized that the magnitude of turbulent mass transfer from the water column to the sediment surface determines the proportion of filter feeders to deposit feeders. They suggest that, at least under food limited situations, deposit feeders predominate in low current speeds and filter feeders are benefited by moderate to high currents and bottom roughness. Such induced changes in water velocities and salinity intrusion probably also affect the rate and distribution of detritus accumulation or processing. The end result of this perturbation would be displaced, if not reduced, sources of food for detritivorous organisms in the channel habitat.

Estuarine channels have traditionally been looked upon as opportune receptacles for urban and industrial wastes due to their usually close proximity to effluent sources and rapid mixing potential. Although there is some consequential urban and rural drainage into subsidiary and blind channels, most of the massive waste discharges occur in mainstem channels. But even these dynamic habitats have a threshold to the amount of wastes which can be accommodated without changes to biological structure. Two categories of common wastes--organic and toxicant--reflect the mechanisms of impact upon channel habitats and associated biota. Organic pollution is manifested primarily through increased chemical or biological oxygen demand within the water column and, with settlement of organic particles, on and within bottom sediments. Since dissolved oxygen is a critical requisite for estuarine organisms' (excluding some microflora) metabolism (see Vernberg and Vernberg 1972 for review), even minor short-term depressions can alter animal behavior and major, long-term declines can result in major community shifts toward a reduced number of more tolerant species. At sufficient concentrations, toxicants such as petroleum hydrocarbons, heavy metals, radioactive isotopes, pesticides, acids, and other chemicals have the potential to directly kill aquatic organisms (i.e., acutely toxic); but more often than not they are present in chronic sublethal concentrations which still influence the distribution and abundance of organisms through degradation of longevity, reproduction, growth, metabolism, and behavior.

Further, more detailed examinations of pollutant effects upon aquatic organisms and communities can be found in reviews such as Bryan (1971) and Warren (1971). Felice (1959) also described a classic case of the influence of domestic and industrial wastes upon the benthic community of San Francisco Bay, an estuary with many parallel features to Pacific Northwest estuaries. Anderson et al.'s (1981) examination of the environmental effects of harbor construction at Steveston, British Columbia, also indicates the synergistic influences of normal environmental perturbation, organic pollution, and dredging and jetty construction on endemic channel communities.

Log transportation ("booming"), dumping, and storage has been a traditional use of estuaries in this region. For example, logs from all along the British Columbia coast are transported to the Fraser River estuary, where almost 5 km^2 of estuarine habitat, most of its shallow reaches of mainstem channels, are developed as "booming grounds" to hold a six-week supply of logs for the local saw and pul mills (Levy et al. 1982). Approximately 1.2 km^2 of the Columbia River estuary is presently utilized for log storage (Pac. NW Riv. Basins. Comm. 1980).

Many studies of the environmental effects of log handling and storage in estuaries have been conducted within the region (Schaumberg 1973; Schuytema and Shankland 1976; Smith 1977; Conlan and Ellis 1979; Sibert and Harpham 1979; Zegers 1979; Levy et al. 1982) and in Alaskan estuaries (Ellis 1970; Pease 1974; Buchanan et al. 1976; Schultz and Berg 1976), while many of the negative impacts documented were particularly associated with littoral habitats, where direct benthic disturbance was caused by grounding logs, log dumping, rafting, and storage in subsidiary and shallow regions of mainstem channels can also produce significant impacts if water exchange from river and tidal currents was low. These were primarily due to the accumulation of bark and log debris on the bottom, causing smothering of benthic organisms and measurable increases in biochemical oxygen demand in the water overlying the debris. Leachates from stored logs and bark deposits may also locally degrade water quality through either direct toxicity or via biological and chemical oxygen demand (Pease 1974; Buchanan et al. 1976; Peters et al. 1976), factors which may be intensified by intermediate salinities (Pease 1974).

Prolonged impacts upon benthic communities resulting from log rafting is often manifested in reduced standing crop and diversity and tends to be restricted to benthic infauna rather than epibenthic organisms except under extreme situations. For example, Smith (1977) illustrated that the abundances of three polychaete annelid species (*Manayunkia aestuarina*, *Pseudoamphicteis neglecta*, *Capitella capitata*), the tubiferous amphipod (*Corophium salmonis*), and oligochaetes were reduced in log raft areas of the Snohomish River estuary, but the epibenthic amphipod *Eogammarus confervicolus* was unaffected. Levy et al. (1982) indicated that epibenthic mysids (*Neomysis mercedis*) and amphipods (*E. confervicolus* and *Corophium* sp.) were either more or equally abundant and isopods (*Gnorimosphaeroma oregonensis*) less abundant in the Point Grey log storage area as compared to the Musqueam Marsa control area; environmental conditions, however, were responsible for some of these differences, and no significant contrasts in growth of chinook salmon fry were evident between the two study areas despite qualitative differences in the fishes' diets.

A final, seldom-considered and even less-evaluated impact upon channel communities is that of extensive exploitation of economically-important species. While habitat reduction or alteration has certainly contributed to the decline of many of our commnmercial or sport fish and invertebrate stocks, overharvesting has certainly played a role in most cases. Given the important role which these consumer organisms (typically upper trophic level carnivores) have upon the structure of channel communities, it may be valid to assume that ecological accommodation has resulted in somewhat different producer and primary consumer assemblages than occurred historically. Pacific salmon, northern anchovy, Pacific herring, and Dungeness crab are examples of exploited species which are suspected to structure their prey assemblages (see Section 9.2); and it must also be concluded that associated pelagic, epibenthic, and benthic assemblages have also responded indirectly to man's exploitation of these predators. The consequence of the recent enhancement efforts upon some of these species, i.e., Pacific salmon, or the protection of other, previously-harvested predators, i.e., seals and sea lions can also be predicted to induce measurable changes in the community because of increased predation upon their preferred food organisms. This has been suggested for hatchery releases of juvenile salmon in Hood Canal (Simenstad et al. 1980) and might also be applied to increased seal and sea lion predation upon crabs and fishes in the Columbia River estuary (Beach et al. 1981). Such holistic food web interactions must be equally considered synergistic with man's other impacts in estuarine channels and, ultimately, within his management strategies for the maintenance or restoration of a specific estuarine channel community.

10.2 UTILIZATION OF AND DEPENDENCE ON CHANNELS BY ECONOMICALLY- AND ECOLOGICALLY-IMPORTANT SPECIES

As illustrated throughout this synthesis, many organisms of economic importance to man or of ecological importance to the estuarine ecosystem can be found utilizing channel habitats. But in the context of estuarine management, the critical question is dependence upon channels to sustain populations of these organisms by providing ample food resources, optimum conditions for growth and/or reproduction, and refugia from predation. Such a definition of utilization in terms of estuarine channels as "critical" habitats requires more knowledge of the functional relationships regulating populations than is usually available.

Utilization of estuarine channels is obvious for many econmically- and ecologically-important species of fishes. But, among these, only a few can be illustrated to be potentially limited by the availability or quality of estuarine channel habitat. Juvenile salmon such as chinook and chum may provide the best example of such a positive functional relationship between estuarine residence and population production (see Section 6.2.2). This may also be the case for Pacific herring (Pearcy and Myers 1974), American shad, and striped bass. But there is some evidence that many species "utilize" offshore environs to a greater extent than estuaries and, as such, occurrence in estuarine channels is merely a product of current transport of planktonic larvae from a large offshore population into the estuary; this may be true of northern anchovy, surf perch, Pacific sand lance, lingcod, English sole, butter sole, and sand sole (Pearcy and Myers 1974). And, while the ecologically-important Crangon spp. shrimps may be highly dependent upon estuarine channel habitats, there is no evidence illustrating that channels provide critical habitats for economically-important Dungeness crab as juveniles, which may be equally or more abundant offshore.

A number of ecologically-important top carnivores such as seals, sea lions, and many of the surface and diving waterbirds are seasonal migrants which behaviorally immigrate to estuarine channels for specific periods of the year. Since there is good evidence that this is associated with optimum foraging and/or reproduction conditions, their population levels may also depend upon this utilization pattern.

10.3 RATES AND PATHWAYS OF RECOVERY FROM SHORT-TERM IMPACTS

Although some manipulations of channels such as extensive dredging can be dramatic in their initial impact, if sustained for only a short interval, biological recovery may also involve only a relatively short time period. Although unverified, it may be assumed that, due to rapid mixing and immigration of pelagic organisms, impact to water column assemblages will be relatively short-lived. Benthic and epibenthic assemblages, on the other hand, will require longer recovery times and may pass through a number of successional stages before attaining pre-impact status. McCauley et al. (1977) documented a readjustment in benthic infauna within a dredged area of Coos Bay, Oregon, after 28 days and within impacted, adjacent areas after 14 days; similarly, infauna at the site of dredge spoil disposal had also recovered from depletion within 14 days. Anderson et al. (1981) described recovery of the benthic community in Steveston Harbor in the Fraser River estuary within one month after dredging. McCauley et al. (1976) also followed the recolonization patterns of four species of polychaete annelids in Coos Bay, Oregon, for eight weeks after maintenance dredging. They found that Capitella capitata dominated the assemblage in recently deposited sediments but not under situations of rapid sediment turnover; Polydora ligni, on the other hand, pervaded where sediments were overturned frequently and where sawdust and wood debris occurred. Steblospio benedicti and Pseudopolydora kempi are common under either recent sedimentation or sediment overturning, perhaps because both can readily vacate their tubes to rebuild new ones quickly. Thus, the rate and pattern of recolonization will proceed as a function of the rate of sediment resuspension or sedimentation as well as the organic content (Bella and Williamson 1979-1980; see also Section 2.5.2). Pequegnat (1975) suggested that meiofaunal constituents of the benthos may be even more sensitive to sediment disruption, as evidenced by changes in generation time, standing stock, and diversity. Although they may be the first colonizers, their intimate relationships with sediment properties and intrinsic short population cycles would dictate that succession of meiofauna assemblages would be prolonged as long as abnormal sedimentation (or removal) persisted.

Unfortunately, such successional patterns have not been well documented in dredging-impact studies in this region. Oliver et al. (1977), however, provided an excellent illustration of benthic succession in a soft-bottom assemblage of small crustaceans and polychaete annelids in Monterey Bay, California. Two phases were evidenced after dredging ceased. The first involved immediate immigration of peracarid crustaceans and settlement of larvae of opportunistic polychaete species, i.e., relatively small-sized taxa with short generation times, low fecundity, and high larval availability. The later phase included gradual reestablishment by less motile crustacenas and less opportunistic polychaete species.

One important thing to remember in considering succession rates and patterns in the temperature waters of the Pacific Northwest is the highly seasonal reproductive schedules of most fauna. As a result, succession is going to be highly mediated by the seasonal availability of propagules of these opportunistic and later successional stage taxa. In addition, benthic assemblages in central regions of large estuaries like the Columbia and Fraser Rivers may never naturally progress beyond the opportunistic species successional stage. Due to the frequent and often extreme fluctuations in salinity regimes, these benthic assemblages are typically limited to species which are tolerant of such random environmental perturbations and persist by being small, capable of wide dispersal and rapid reproduction, and extremely euryhaline.

10.4 METHODS OF CHANNEL RESTORATION AND REHABILITATION

Unlike the recent support for estuarine marsh restoration (Josselyn 1982; but see Race and Christie 1982 for caveats), restoration and rehabilitation of channels is seldom considered among available options in estuarine habitat management. Dorcey et al.'s (in press) analysis of the history, status, and management options of estuarine sloughs, specifically Tilbury Slough in the Fraser River estuary, presents one of the few discussions of restoration and enhancement strategies applicable to such estuarine channel and associated habitats (e.g., marshes). Among the rehabilitation options specific to the area's channels were: 1) breaching of remnant dykes to increase flushing and passage of juvenile salmon; 2) dredging of the mouth and channel to arrest infilling and maintain circulation; 3) dredging of side (blind) channels to increase juvenile salmon utilization; and, 4) stabilization of water levels through flow control structures and selected channel creation.

In addition to these means of restoring the habitat to a viable, productive environment, management must involve removal or mediation of the sources of degradation and protection of the self-cleansing mechanisms. In the case of Tilbury Slough, as in many similarly-developed estuarine channels in the Pacific Northwest, exogenous influences such as pollutant sources eliminate some of the more viable options (i.e., opening up flow from the former, upriver end of the channel). In all cases, however, restoration must be accompanied by changes in those uses which led or contributed to the channel's deterioration. Pollutant sources must be eliminated or diverted. Structures (i.e., docks, training walls, wharves) and practices (i.e., log dumping and storage) which promote abnormal sedimentation and scouring must be discouraged.

There are presently active management policies promoting or practicing mitigation as a means of compatibly incorporating necessary estuarine development into the natural environment without precluding such activity (Ashe 1982). As such, mitigation can take on two goals: 1) the creation, restoration, or enhancement of an estuarine area to maintain the functional characteristics and processes of the estuary; and, 2) the creation or restoration of another area of similar biological potential to ensure that the integrity of the estuarine ecosystem is maintained. While the first goal is compatible with maintenance of a viably-functioning estuarine channel community, the second goal should be approached judiciously. Destruction or debilitative modification of any natural habitat, particularly channels so integral to an estuary's circulation, by creation of a supposedly equivalent habitat cannot be justified with the existing technology. This approach to mitigation originated from relatively successful salt marsh restoration projects in east coast estuaries, but man-made marshes in west coast estuaries have yet to be proven comparable replacements for natural marshes (Race and Christie 1982). Although restoration of diked, filled, or modified channels is a worthwhile objective of contemporary estuarine management, devaluing existing channels in exchange for the unpredictable results of these projects is still a dubious strategy.

10.5 RESEARCH GAPS AND PRIORITIES

Despite the profusion of knowledge of estuarine channels in the Pacific Northwest, illustrated by the bulk of the Literature Cited section, we find our understanding of the role of these habitats in the estuarine ecosystem to be limited. In most cases this is because this vast accumulation of data is predominantly descriptive and qualitative. That which is quantitative is typically oriented toward a particular taxa and seldom of a scope encompassing other organisms of the community, environmental conditions, or functional relationships among them. Future research must address this lack of holistic approaches, particularly when evaluating the dependence of important biota upon key functional processes. Despite the intent of this synthesis to identify the role of estuarine circulation, salinity gradients, nutrient and material fluxes, and sediment structure in determining the composition, distribution, and standing stock of estuarine biota (Section 1.1), few such functional relationships have been verified though many have been hypothesized. The following research proposals are designed to elucidate, test, and quantify these "conceptual hypothesis models" in terms of the functioning of estuarine channel systems, their relationship to overall estuarine processes, and the implications of estuarine management options.

1. Prepare comprehensive analysis of historical trends in channel habitat demography (extent and morphology) for all major Pacific Northwest estuaries where data exists; interpret documented changes relative to natural and anthropogenic processes.

2. Vertically-stratified, three-dimensional mathematical modeling of circulation in a prominent, representative Pacific Northwest estuary should be conducted with considerable field calibration in order to better understand the effect of river discharge and estuary bathymetry upon salinity intrusion and sedimentation. Various development scenarios affecting parameters such as riverine discharge (i.e., dams), bathemetry (i.e., dredging), or geomorphology (i.e., jetty construction) could be simulated for optimum assessment of effects upon circulation.

3. Conduct intensive, vertically-stratified sampling of pelagic and epibenthic zooplankton over diel periods at representative channel locations through the estuarine gradient. If performed concurrently with field calibration of the three-dimensional circulation model (#2 above), the resulting documentation of diel patterns in zooplankton distribution and standing stock could be correlated with cycles in tidal and current velocity, salinity distributions, and mixing processes.

4. As in Healey's (1982) estimation of the ultimate (i.e., to adult return) survivorship of chum salmon utilizing the Nanaimo River estuary, the

relative importance of estuarine channel attributes must be evaluated in terms of the total cost to the salmon population. Similarly, different patterns of channel utilization by juvenile salmon (e.g., extended residence, inshore/offshore movements) must be examined relative to these attributes. Although there is often opportunity for "natural" experiments, the lack of control over dependent variables often inhibits interpretation. For this reason, manipulation experiments should be undertaken to isolate independent variables affecting patterns of channel utilization. Examples include equal releases of marked groups of fish at different points along the estuarine gradient or different density or fish-size releases just upstream of the estuary and recapture of the marked fish at the mouth or just outside the estuary.

5. Despite strong evidence that food webs of estuarine channel communities are based predominantly upon detritus, there is little data substantiating this hypothesis (see Section 9.1). Techniques such as stable carbon isotope analysis should be applied to primary producers, inputs of dissolved and particulate organic and dissolved inorganic carbon from exogenous sources, detritus accumulations, and dominant consumer organisms in estuarine channels in order to evaluate the sources and pathways of organic carbon leading to the endemic food web.

6. Similar to determining causal mechanisms of utilization of estuarine channels by juvenile salmon (#4 above), the factors influencing structure, distribution, and standing stock of benthic and epibenthic assemblages cannot be easily elucidated from highly variable field measurements; separation of confounding effects of natural physical and chemical influences from those of pollution are also usually intractable. Functional relationships between physiochemical variables and larval settlement, feeding and other critical behavior, reproduction, and survival can be resolved only through experimental means. Organisms such as polychaete annelids, harpacticoid copepods, gammarid amphipods, mysids, and crangonid shrimps should be tested under controlled replicatable conditions indicative of estuarine channel benthic environs, both as individual species and life history stages as well as characteristic mixed-taxa assemblages. This approach achieves its ultimate applicability in the form of ecosystem microcosms which, although subject to a number of shortcomings (Harte et al. 1980; Simenstad et al. 1982) can be a very effective method of environmental impact assessment and ecological elucidation (T.P. Smith 1980).

7. The importance of the null zone in the concentration of detritus has been suggested by studies of water column primary production and both pelagic and epibenthic zooplankton (see Chap. 5). But the processes accounting for detritus entrainment and processing in the null zone of the region's estuaries are little understood. Both vertical and horizontal distributions of detritus particles and associated water chemistry characteristics (i.e., DOC, DON, ATP) should be sampled seasonally in relation to circulation parameters in an estuary with a well-defined null zone. As in documenting zooplankton distribution processes (#3 above), coupling with the three-dimensional circulation model (#2 above) would also expand the potential of similarly explaining detritus cycling and utilization by physical circulation processes.

Appendix D provides a list of research groups/organizations currently conducting research in estuarine channel habitats in the Pacific Northwest.

10.6 SUMMARY

Although they are classically avoided in most research, due to the complexity and dynamic nature of the physiochemical environment, channel habitats in Pacific Northwest estuaries obviously support unique populations of economically- and ecologically-important biota. This bonding takes form as routes for organism movement and migration, conduits of material transport, and sources of replenishment for sediments, nutrients, food particles, and organism recruits. All estuarine habitats are integrated through the estuary's articulated system of mainstem, subsidiary, and blind channels, and the principal linkages with terrestrial and marine ecosystems occur through the mainstem channels. In addition to this critical role as the estuary's circulatory system, channels act as critical nursery habitats for organisms such as juvenile Pacific salmon and Pacific herring; as opportune foraging and resting habitats for migrant birds and marine mammals; and as the focal point of detritus entrainment, accumulation, and processing in the estuary.

Management of any estuarine resource or exogenous resources which derive benefit from a well-functioning estuary cannot occur without consideration and management of estuarine channels. But the state of our knowledge of estuarine channel communities and processes and of their management is lagging far behind that of the other major estuarine habitats. This document describes what Dorcey and Hall (1981) would define as the "descriptive knowledge" necessary for input into management decisions. Unfortunately, there is also a second category of requisite information, that of the "functional knowledge" of how the channel's biotic and abiotic processes operate and interact, which we have barely begun to develop. Essentially all the studies described herein have been derived from inventorying or monitoring types of investigative activities. Any interpretation of system processes has merely been the result of deductive analyses. Genuine functional knowledge requires a different approach, that of generating testable hypotheses and experiments. Such experimental research offers our only view of causal mechanisms, and the process of sequentially testing alternative hypotheses is our only means of exploring the complex interrelationships affecting channel communities. Effective management decisions require this functional knowledge and, as advocated by Dorcey and Hall, experimental management and research are the only source of functional knowledge. It is hoped that, in addition to synthesizing our descriptive knowledge of estuarine channel communities in the Pacific Northwest, this community profile might provide the impetus for the necessary steps to the experiments which are ultimately necessary for effective management of our region's estuaries.

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APPENDIX A

Glossary of Terms

GLOSSARY OF TERMS

Advection - Local change in a property of a system that takes place as a result of a current, as of air or water; includes transport of water vapor, heat, sediment load, salinity (Proctor et al. 1980).

Alkalinity - The capacity of a water mass to accept protons, i.e., hydrogen ions.

Anadromous - Migrating up rivers from the sea to breed in fresh water.

Anastomosing - Branching, interlacing, intercommunicating, thereby producing a netlike or braided appearance.

Angular - A roundness grade showing very little or no evidence of wear, with edges and corners sharp (Am. Geol. Inst. 1976).

Autotrophic - Self-nourishing; referring to organisms that are capable of constructing organic matter with high-energy bonds from inorganic substances for their food supply by photosynthesis or chemosynthesis.

Bar - An elongated landform generated by waves and currents, usually running parallel to shore, composed predominantly of unconsolidated sand, gravel, cobbles, stones and rubble and with water on two sides.

Bed - Bottom of the channel.

Bed Load - Sediment particles and other debris rolled along the bottom by moving water.

Benthic - Relating to the bottom of the body of water, i.e. animals, living within or directly upon the substrate.

Benthivore - Organism which feeds on benthic flora and fauna.

Bight - A bend, curve, or indentation in the shore of a sea, including the body of water bounded by such a coastal form.

Boulder - Rock fragment with diameter larger than 60.4 cm (Cowardin et al. 1979).

Cavitation - Corrasive and corrosive effect of collapsing of bubbles produced by a decrease of pressure to increase of water velocity (Bernoulii effect) at point where pressure is increased to decrease of velocity (Am. Geol. Inst. 1976)

Channel - An open conduit either naturally or artificially created which periodically or continuously contains moving water, or which forms a connecting link between two bodies of water (Langbein and Iseri 1960).

Channel Bank - The sloping land bordering a channel, which typically has a steeper slope than either the bottom of the channel or the adjacent land (Cowardin et al. 1979).

Cobble - Rock fragments with diameters between 7.6 cm and 25.4 cm (Cowardin et al. 1979).

Competence - Maximum size of particles of given specific gravity which a water mass will move at a given velocity.

Consumer - Heterotrophic organism, chiefly animals, which ingest other organisms or particulate organic matter.

Coriolis Effect - The effect of the earth's rotation to deflect water masses to the right in the northern hemisphere and to the left in the northern hemisphere.

Corrasion - Mechanical erosion performed by moving agents, generally by the impact or grinding action of particles in water.

Corrosion - Chemical erosion which results from the reaction of water and rocks on the surface of the land.

Critical Erosion Velocity - Lowest velocity at which grains of a given size, loose on the bed of a channel, will move.

Decomposer - An organism that breaks down dead organic matter into simpler constituents for its nutrition.

Demersal - Nektonic fauna living on or closely associated with the bottom; typically refers to fishes, where epibenthic refers to invertebrate fauna.

Dendritic - A drainage pattern characterized by irregular branching in all directions with the tributaries joining the main channel at all angles (Am. Geol. Inst. 1976).

Density - Abundance of organisms per unit area or volume.

Deposit Feeder - Organism, typically benthic, which is either somewhat selective or almost completely unselective in feeding; includes organisms which sweep the surface or use ciliary tracts along extensile tentacles.

Detritus - Finely divided material of organic or inorganic origin which is either suspended in the water column or, in the case of large particles, accumulated on the bottom.

Diffusion - The spreading out of molecules, atoms, or ions in a water mass in directions tending to equalize concentrations in all parts of the system.

Diversity - Term or measure used to describe the species-abundance distribution of a biotic assemblage or community; both the number of species and the evenness of their abundances contribute to the term (Pielou 1977).

Elutriate - The fluid product of mixing water, or a water acid solution, with sediment, allowing settling over a varying amount of time and decanting the resulting solution.

Epibenthic - Associated primarily with the surface of the bottom but also with the water column directly above the bottom.

Euhaline - Associated with mouth or extreme salinity, i.e., 30-40 ppt, region of estuary (Symp. Class. Brack. Wat. 1959).

Facultative (Feeder) - An organism which is not functionally constrained to feeding on one general type of plant or animal but may feed on diverse prey from several trophic levels.

Flocculation - Aggregation of small suspended particles due to ionic changes brought on by contact with seawater.

Fluviatile - Belonging to a river or produced by river action (Am. Geol. Inst. 1976).

Flow Ratio - Ratio of volume of upland water entering the estuary during a tidal cycle to its tidal prism.

Fluvial - Of, or pertaining to, rivers.

Food Web - The pattern and sequence of feeding interrelationships among the organisms of a community, from reducer and producer organisms to the highest carnivores.

Food Web Linkage - The trophic connection between food web node.

Food Web Module - Interacting species that seem dependent upon specific prey resources, give evidence for evolved modification for use of, or association with, these resources, and that disappear upon removal of a strongly interacting species (or appear with its addition) constitute a module (Paine 1980).

Food Web Node - Species, taxon, or functional feeding group constituting a unique prey or predator compartment in a food web.

Gravel - Rock fragments with diameters between 2 mm and 7.6 cm (Cowardin et al. 1979).

Littoral - Pertaining to the shore zone between extreme high and low tide levels during spring tides.

Meroplankton - Planktonic stages (eggs and larvae) of organisms which in later life will become members of the benthos or nekton.

Mesohaline - Associated with upper reaches or intermediate salinities, i.e., 5-18 ppt, region of estuary (Symp. Class. Brack. Wat. 1959).

Nektonic - Capable of swimming against normal wave and current action, i.e., self-propelled.

Neritic - Shallow surface water zone extending from the high-tide mark to the edge of the continental shelf.

Neuston - Organisms associated with the surface film of the water.

Obligate (Feeder) - Organism constrained by morphology or behavior to feeding on one general type of plant or animal.

Omnivore - Organism which feeds on both plant and animal matter.

Oligohaline - Associated with head or low salinity, i.e., 0.5-5 ppt, region of estuary (Symp. Class. Brack. Wat. 1959).

Pelagic - Characteristic of the water column and not in association with the bottom.

Phi Units - Units of particle or grain size where $\phi = -\log_2$ dia (mm).

Planktivore - Organism which feeds on suspended zooplankton and nekton.

Polyhaline - Associated with middle and lower reaches of estuary, typically with salinities between 18-30 ppt (Symp. Class. Brack. Water 1959).

Primary Production (Rate) - Measure of carbon fixed per unit area per unit time by photosynthetic organisms (producers); usually expressed as g C m^{-2} hr^{-1}.

Rheotaxis - Movement of an organism in which a water stream or current is the directive stimulus.

Saline - Possessing a high degree of salinity, i.e., more than 3°/₀₀ (Am. Geol. Inst. 1976).

Salinity - The total amount of dissolved solid material (in grams) contained in one kilogram of water, expressed as °/₀₀ (ppt). For this measurement all organic matter is oxidized, all carbonate converted to oxide, and all bromide and iodide replaced by chloride (Sverdrup et al. 1942; colloquial - the saltiness of a body of water).

Sand - Coarse-grained mineral sediments with diameters between 74 µm and 2 mm (Cowardin et al. 1979).

Spring Tides - The highest high and lowest low tides during the lunar month.

Standing crop - Term applied to biomass of organisms per unit area or volume.

Standing stock - Term used to describe combined concept of density and standing crop.

Stone - Rock fragments with diameters between 25.4 cm and 60.9 cm (Cowardin et al. 1979).

Subaerial wetlands - Wetland habitats which lie between mean low water and mean high water.

Sublittoral - Pertaining to the marine zone between extreme lowest low tidal level and the margin of the continental shelf.

Subrounded - A roundness grade in which considerable wear is evident, with edges and corners rounded to smooth curves and the area of the original faces considerably reduced (Am. Geol. Inst. 1976).

Suspension feeder - Organism which processes water for food, either passively (benthic) or actively (pelagic) entraining phytoplankton and other microscopic organisms and suspended detritus.

Thigmotaxis - Movement of an organism in which contact with a solid body (i.e., algae, bottom sediments, rocks, pilings) is the directive stimulis; also called stereotaxis.

Tidal amplification (factor) - Local tidal range as a function (divided by) the tidal range at or near the mouth of the estuary.

Trophic - Related to food, feeding, and nutrition.

Trophic level - A group of organisms in a food web that secures food in the same general manner.

Volatile solids - Products, exclusive of moisture, given off as gas and vapor as determined by definite prescribed methodology; measure of organic content.

APPENDIX B

Sediment Classification Schemes

Appendix Table B-1. Various schemes of unconsolidated sediment particle classification (Source: U.S. Army Corps Engineers 1973).

Wentworth Scale (size description)		Phi Units ø*	Grain Diameter d(mm)	U.S. Standard Sieve Size	Unified Soil Classification (USC)	
Boulder						
		-8	256.0		Cobble	
Cobble			76.2	3 in.		
		-6	64.0		Coarse	Gravel
			19.0	3/4 in.		
Pebble			4.76	No. 4	Fine	
Granule		-2	4.0		Coarse	Sand
Sand		-1	2.0	No.10		
	Very Coarse	0	1.0		Medium	
	Coarse	1	0.5			
	Medium		0.42	No.40		
		2	0.25		Fine	
	Fine	3	0.125			
	Very Fine		0.074	No.200		
Silt		4	0.0625		Silt or Clay	
Clay		8	0.00391			
		12	0.00024			
Colloid						

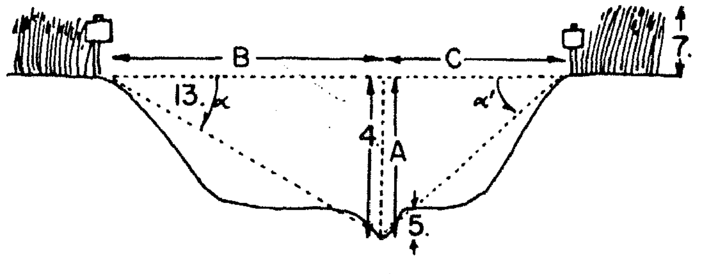
* ø = $-\log_2 d$(mm)

APPENDIX C

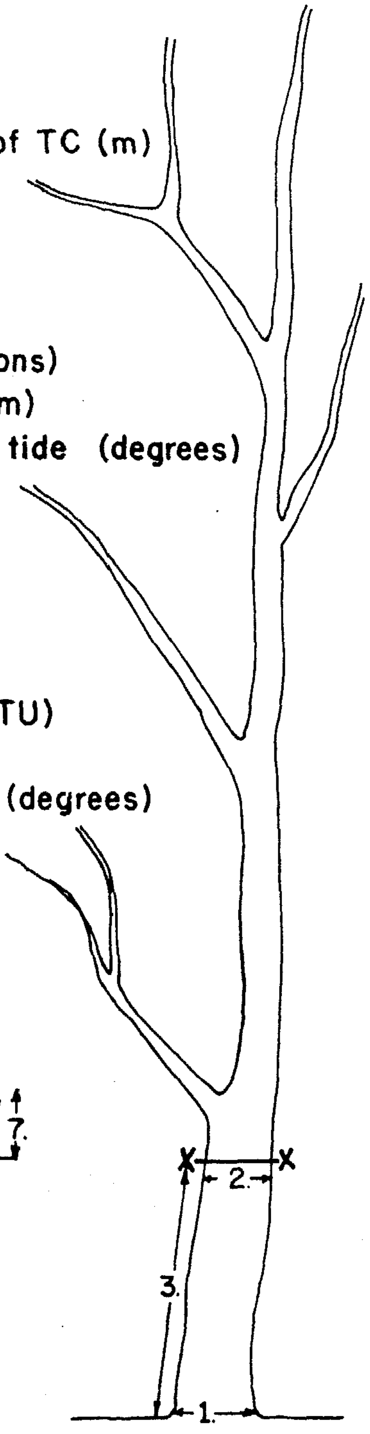
Tidal Channel Characteristics Measurements
(from Levy and Northcote 1981)

Measured Tidal Channel (TC) Characteristics

1. TC mouth width (m)
2. Width of TC at sampling station (m)
3. Distance from sampling site to mouth of TC (m)
4. TC depth (m)
5. Trough depth (cm)
6. TC length (m)
7. Average sedge height (m)
8. Average sediment particle size (microns)
9. Distance to nearest subtidal refuge (m)
10. Angular deflection to prevailing flowing tide (degrees)
11. Channel order
12. Sub-channel length (m)
13. Angle of sedge bank (degrees)
14. Slope of the tidal change (m/hr)
15. Height of the high tide (m)
16. Turbidity of the water at low tide (NTU)
17. Area of the TC (m^2)
18. Compass heading of main axis of TC (degrees)
19. Relative elevation of TC bottom (m)
20. Elevation of surrounding bank (m)
21. Area of refugia at low tide (m^2)
22. Length of time TC submerged (hr)



cross-section



Measurement of Tidal Channel Habitat Characteristics

Fish catch results from the May 10-17 surveys were compared statistically with habitat characteristics of tidal channels to assess which characteristics were associated with high numbers of fish in different tidal channels. The characteristics used in the analysis were chosen to be easily measurable either directly at the sampling site or in the laboratory, or indirectly from Fraser River Delta Project Maps. Figure 5 shows several of the tidal channel characteristics and Table 13 supplies numerical values. The following measurements were taken and included in statistical analyses:

1. Width of the tidal channel mouth in meters (MTHWDTH) - measured in the field from one tidal channel bank to the other perpendicular to the axis of the channel.

2. Width at the sampling site in meters (STNWDTH) - measured in the field from one tidal channel bank to the other perpendicular to the axis of the channel.

3. Distance from the sampling site to the tidal channel mouth in meters (MTHDIST) - measured with a map measure from the Fraser River Delta Series Maps.

4. Tidal channel depth in metres (CHNDPTH) - measured in the field at low tide. A rope was stretched between the stakes at the level of the bank and a 3-meter pole, graduated at 5 cm intervals, was positioned vertically in the deepest part of the tidal channel. The height at which the rope bisected the pole was recorded as the tidal channel depth.

5. Trough depth in centimeters (TRODPTH) - the residual tidal flow near low tide frequently scoured a trough in the bottom of the tidal channel which varied in depth between sampling sites.
   This depth was measured with a ruler during periods of low slack tide between June 7-13, 1979.

6. Length of the tidal channel in meters (TCLNGTH) - measured with a map measure from the Fraser River Delta Series Maps. The length was defined from the position of the sampling site to the furthest point on the 0 foot geodetic perimeter of the tidal channel.

7. Height of surrounding marsh plants in meters (HTSEDGE) - measured in the field during a one week period at the beginning of June, 1979 using a 3-meter pole graduated in 5 cm intervals.

8. Mean sediment particle size (SEDSIZE) - replicate sediment samples were obtained on June 12, 1979 at all 18 tidal channel sampling sites. Samples of the upper 1 cm of sediment were collected with a trowel close to the center trough of the tidal channels and transported to the Geochemistry Lab, U.B.C., in Whirl Pak Bags. The samples were dried in an oven in drying bags and then broken up with a mortar and pestle. Individual samples were then placed on the uppermost (coarsest) of a series of 6 sieves and shaken for 5 minutes. The fractions of sediment were weighed and the proportion of sediment in a given size range calculated as a fraction of the total sample weight. The average particle size in a given fraction was assumed to be half-way between the surrounding sieve sizes. The proportion of sediment in a given fraction was multiplied by the average particle size to obtain weighted proportions of sediment which were then summed to give an estimate of the mean particle size. The average value of 2 replicates was used in the statistical analyses and is shown in Table 13.

9. Distance to nearest sub-tidal refuge in meters (REFDIST) - determined as the distance from the sampling site to the nearest slough (sub-tidal) habitat capable of maintaining juvenile salmon at low tide when no water occurred in the tidal channels. This distance was measured off Fraser River Delta Maps with a map measure.

10. Angular deflection to prevailing flowing tide in degrees (ANGDEFL) - the angle of the axis of the tidal channel at the mouth to the direction of the flooding tide in the slough (Figure 5) was measured off the Fraser River Delta Maps with a protractor.

11. Tidal channel order (TCORDER) - tidal channels were classified according to the following characteristics:

ORDER	CHARACTERISTICS
1	large sub-tidal slough or reach which never dewaters at low tide.
2	large channel which experiences high velocity tidal flows and usually does not dewater at low tide.
3	inter-tidal channel which branches off a 2nd order channel or slough and usually dewaters completely at low tide.
4	small inter-tidal channel which branches off a 2nd or 3rd order channel and always dewaters at low tide.

12. Total sub-channel length in meters (SUBCHNL) - the length of all tributaries flowing into the tidal channels was measured with a map measure. Only those tributaries deeper than the 0-foot contour were included.

13. Average angle of the sedge bank in degrees (ANGBANK) - determined in the field indirectly through measurement of parameters A, B and C (shown on Figure 5) and calculation of angles α and α' where $\alpha = \tan^{-1} A/B$ and $\alpha' = \tan^{-1} A/C$. The mean value for these 2 angles was used to give a measure of the relative slope of the tidal channel banks.

14. Slope of the tidal change in meters per hour (TIDSLOP) - the difference between the height of the predicted high and low tides at Point Atkinson was divided by the length of time between these two tides to give a measure of the rate of tidal flow for the dates sampling took place.

15. Height of the high tide in meters (HTHTIDE) - the predicted levels of the high tide at Point Atkinson for the dates sampling took place were obtained from tide tables.

16. Turbidity of the trough water at low tide in nephelometric turbidity units (WATURB) - water sampling took place at low tide on June 12, 1979 at all 18 tidal channel sampling sites. Sub-surface samples were obtained from the trough of the tidal channel in 250 ml plastic sample jars. Care was taken to avoid disturbing the sediment upstream of the sampling site. Turbidity levels were later determined in the laboratory with a Hach Turbidimeter.

17. Area of the tidal channel in square meters (TCAREA) - measured by planimetry from the Fraser River Delta Series maps. The margins of the tidal channels were defined by the 0-foot geodetic contour.

18. Compass heading of the main axis of the tidal channel in degrees (COMPASS) - the main axis of the tidal channel was drawn onto Fraser River Delta maps and the difference between this line and the North axis was measured with a protractor.

19. Elevation of the tidal channel bottom in meters (TCELEV) - the depth of water in the tidal channels was measured with a 3-meter graduated staff gauge at all eighteen sites over a 40 minute period near high tide on June 14, 1979. The location of the deepest part of the channel was marked with a previously deposited anchor and float. Since all measurements were conducted at a time when the water level was static, measured differences reflected variations in bottom

elevation. The measured water depths were subtracted from the level of the predicted high tide at Point Atkinson to give a measure of the absolute elevation of the tidal channel bottom. The measurements were repeated on two consecutive high tides to compare results. Since the relative ranking of bottom elevation was consistent, only the June 14 results are shown in Table 13.

20. Elevation of the surrounding bank in meters (BNKELEV) - the average of two spot heights nearest the sampling site was determined from the Fraser River Delta Series maps. This served to give a measure of the absolute elevation of the surrounding marsh habitat above 0 foot geodetic elevation.

21. Area of low elevation refuges in square meters (AREAREF) - the area of sub-tidal pools in the tidal channels was planimetered from the Fraser River Delta Series maps. These areas were bounded by dashed lines and indicated low elevation depressions in the tidal channels which contained water at low tide.

22. Time of submergence prior to sampling in hours (TIMESUB) - calculated by plotting tidal curves (predicted tide height at Point Atkinson vs. time) and defining the period of tidal channel submergence prior to sampling based on the measured tidal channel bottom elevations (no. 19 on p. 13). The number of hours at which the predicted tide level was greater than the measured elevations was extrapolated off the tidal curves.

Appendix Table C-1. Measured tidal channel habitat characteristics. For explanation of terms and units of measurement, see text.

Tidal Channel Characteristics	SAMPLING SITES Woodward Island						Barber Island					Ladner Marsh					Roberts Bank	
	W1	W2	W3	W4	W5	W6	B1	B2	B3	B4	B5	D1	D2	D3	D4	D5	F1	F2
MTHWDTH	17.0	29.0	13.5	4.5	14.5	21.5	15.0	13.0	10.5	11.5	6.0	13.0	19.5	9.5	11.5	11.5	10.5	5.5
STNWDTH	9.9	28.0	12.9	7.9	8.3	12.1	11.8	10.8	11.3	12.3	3.9	9.7	11.6	6.9	8.7	20.4	7.2	7.7
MTHDIST	192	53	85	30	35	1128	55	65	165	132	4	9	282	28	90	98	40	65
CHNDPTH	1.75	1.95	1.38	1.19	1.74	1.31	1.69	1.96	1.68	2.13	1.57	2.16	2.05	1.90	1.77	2.27	1.18	1.88
TRODPTH	9.0	15.0	5.0	5.0	6.0	5.0	6.5	3.5	17.5	8.0	3.0	6.0	14.5	7.0	9.0	24.5	6.0	6.0
TCLNGTH	495	870	480	391	566	234	352	370	891	315	346	770	463	215	376	480	414	533
HTSEDGE	0.95	1.05	1.10	1.15	0.95	1.05	0.85	0.85	0.90	0.35	0.90	1.10	1.10	0.95	1.35	1.40	0.75	0.60
SEDSIZE	192	108	98	75	155	89	79	83	77	105	87	72	96	84	100	80	80	143
REFDIST	219	63	489	522	45	1143	70	189	188	216	144	13	291	49	217	228	416	290
ANGDEFL	79	56	57	57	46	57	96	79	20	78	65	102	33	111	0	0	60	77
TCORDER	3	2	3	3	3	2	3	3	3	3	4	3	3	3	3	2	3	3
SUBCHNL	474	2210	838	311	476	492	659	500	1229	495	75	200	495	78	252	227	983	439
ANGBANK	19.4	8.6	12.5	17.0	26.3	12.6	16.3	20.2	16.4	19.8	38.8	24.1	24.2	29.0	22.5	13.4	19.0	26.8
TIDSLOP May 10-13	0.44	0.44	0.44	0.44	0.44	0.44	0.49	0.49	0.49	0.49	0.49	0.48	0.48	0.48	0.48	0.48	0.46	0.46
TIDSLOP May 14-17	0.49	0.49	0.49	0.49	0.49	0.49	0.36	0.36	0.36	0.36	0.36	0.44	0.44	0.44	0.44	0.44	0.49	0.49
HTHTIDE May 10-13	4.2	4.2	4.2	4.2	4.2	4.2	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.1	4.2	4.2
HTHTIDE May 14-17	4.1	4.1	4.1	4.1	4.1	4.1	3.7	3.7	3.7	3.7	3.7	3.9	3.9	3.9	3.9	3.9	4.1	4.1
WATURB	110	77	25	30	125	130	160	22	100	120	52	67	46	23	36	76	80	57
TCAREA	4608	24071	6197	3084	4097	2778	3855	4385	9950	4311	1180	3893	2694	2044	2323	8240	4617	3214
COMPASS	197	95	103	99	263	121	40	114	85	328	122	8	84	143	33	79	144	266
TCELEV	1.61	1.41	1.95	2.09	1.68	2.19	1.67	1.91	1.62	1.68	1.96	1.81	1.86	2.12	1.94	1.58	2.34	2.21
BNKELEV	0.2	0.3	0.2	0.3	0.4	0.6	0.6	0.8	0.9	0.5	1.1	0.9	1.2	0.9	1.0	1.2	0.0	0.6
AREAREF	37	2183	632	74	74	9	46	0	1623	37	0	0	46	56	0	1208	418	0
TIMESUB May 10-13	17.43	17.67	16.49	16.10	17.24	15.83	16.02	15.55	16.12	16.00	15.45	15.86	15.76	15.22	15.59	16.34	15.02	15.32
TIMESUB May 14-17	15.75	16.13	15.12	14.86	15.62	14.68	16.05	15.57	15.15	15.51	16.23	15.56	15.46	14.96	15.31	16.00	14.47	14.71

APPENDIX D

Summary of Current Research and Research Groups/Centers Addressing Estuarine Channel Ecology or Effects of Alteration of Channel Habitats

Estuarine Channel Research in Pacific Northwest

Organization: Oregon Institute of Marine Biology
University of Oregon

Address: Oregon Institute of Marine Biology
University of Oregon
Charleston, Oregon 97420

Contact(s): Daniel Varoujean, Paul Rudy Jr.

Type of Research: general estuarine ecology

Location: Coos Bay

Organization: Oregon Department of Fish and Wildlife

Address: Oregon Department of Fish and Wildlife
Oregon State University
Extension Hall 303
Corvallis, Oregon 97331

Contact(s): Daniel Bottom, James Lichatowich, Kim Jones, Peggy Herring

Type of Research: estuarine utilization by juvenile salmonids

Location: Oregon coastal estuaries, Coos Bay

Organization: Department of Botany and Plant Pathology
Oregon State University

Address: Department of Botany and Plant Pathology
Oregon State University
Corvallis, Oregon 97331

Contact(s): C. David McIntire

Type of Research: benthic primary production; eelgrass production and physiology; structure and production of epiphytic algae

Location(s): Columbia River estuary; Netarts Bay

Organization: Department of General Science
Oregon State University

Address: Department of General Science and, Marine Science Center
Oregon State University Newport, Oregon 97365
Corvallis, Oregon 97331

Contact(s): Robert Worrest, Danil Hancock

Type of Research: ecology of estuarine diatoms

Location: Yaquina Bay

Organization: Department of Geography
Oregon State University

Address: Department of Oceanography
Oregon State University
Corvallis, Oregon 97331

Contact(s): Robert Frenkel, Theodore Boss

Type of Research: saltmarsh community ecology; introduced species of estuarine macrophytes

Location: Siuslaw River estuary

Organization: School of Oceanography
Oregon State University

Address: School of Oceanography and, Marine Science Center
Oregon State University Newport, Oregon 97365
Corvallis, Oregon

Contact(s): Lawrence Small, Charles Miller, Robert Holton, Jefferson Gonor
James Good

Type of Research: water column primary production; phytoplankton assemblage structure; zooplankton grazing on estuarine phytoplankton; pelagic zooplankton assemblage structure and dynamics; benthic infauna assemblage distribution and structure

Location(s): Columbia River estuary, Yaquina Bay, Coos Bay

Organization: Hammond Laboratory
National Marine Fisheries Service

Address: Hammond Laboratory
National Marine Fisheries Service
P.O. Box 155
Hammond, Oregon 97121

Contact(s): Robert McConnell, George McCabe, Robert Emmett

Type of Research: fisheries ecology; distribution, abundance, and food habits of juvenile salmonids and Dungeness crab

Location: Columbia River estuary

Organization: Battelle Marine Research Laboratory
Battelle Memorial Institute Northwest

Address: Battelle Marine Research Laboratory
439 West Sequim Bay Road
Sequim, Washington 98382

Contact(s): James Young, Walter Pearson, Jack Anderson, Charles Gibson

Type of Research: estuarine ecology of benthic infauna, pelagic zooplankton and fishes; effects of oil pollution on estuarine communities

Location: Strait of Juan de Fuca and northern Puget Sound

Organization: Fisheries Research Institute
University of Washington

Address: Fisheries Research Institute WH-10
College of Ocean and Fishery Sciences
University of Washington
Seattle, Washington 98195

Contact(s): Charles Simenstad, Robert Wissmar, Ernest Salo, Quentin Stober, Bruce Miller

Type of Research: estuarine utilization by juvenile salmonids; food web structure of Pacific Northwest estuaries; structure and dynamics of epibenthic and neritic zooplankton communities in estuaries; estuarine fish assemblage structure

Location: Hood Canal, Puget Sound and component estuaries, Grays Harbor, Columbia River estuary

Organization: School of Fisheries
University of Washington

Address: School of Fisheries WH-10
College of Ocean and Fishery Sciences
University of Washington
Seattle, Washington 98195

Contact(s): David Armstrong, Kenneth Chew, Ronald Thom, Jack Word

Type of Research: basic biology and ecology of estuarine crustaceans and molluscs; early life history (larval) of economically important crustaceans; mariculture of estuarine organisms

Location: Grays Harbor, Puget Sound and associated estuaries

Organization: Department of Oceanography
University of Washington

Address: School of Oceanography WB-10
College of Ocean and Fisheries Sciences
University of Washington
Seattle, Washington 98195

Contact(s): Joe Creager, Chris Sherwood, David Jay, T. Saunders English, Peter Jumars, Arthur Nowell

Type of Research: estuarine sedimentology and circulation; estuarine zooplankton and larval fish distribution, abundance, and ecology; benthic infauna and epifauna ecology

Location: Columbia River estuary, Puget Sound and associated estuaries

Organization: Huxley College of Environmental Studies
Western Washington University

Address: Huxley College of Environmental Studies
Western Washington University
Bellingham, Washington 98225

Contact(s): William Summers, Bert Webber

Type of Research: ecology of estuarine and nearshore marine algae and benthic invertebrate communities

Location: northern Puget Sound estuaries

Organization: Department of Oceanography
University of British Columbia

Address: Department of Oceanography
University of British Columbia
Vancouver, British Columbia V6T 2B1
Canada

Contact(s): Brenda Harrison

Type of Research: ecology of estuarine benthic and epibenthic invertebrate communities

Location: Fraser River estuary

Organization: Department of Botany
University of British Columbia

Address: Department of Botany
University of British Columbia
Vancouver, Britich Columbia V6T 2B1
Canada

Contact(s): Paul Harrison, Richard Bigley

Type of Research: seagrass (Zostera spp.) community ecology

Location: Strait of Georgia estuaries, northern Puget Sound

Organization: Westwater Research Centre
University of British Columbia

Address: Westwater Research Centre
University of British Columbia
Vancouver, British Columbia V6T 1W5
Canada

Contact(s): Thomas Northcote, David Levy, Anthony Dorcey, Kenneth Hall

Type of Research: estuarine utilization by juvenile salmonids; management of estuarine habitats; effects of log rafting, diking and filling, and construction of training walls

Location: Fraser River estuary

Organization: Department of Biological Sciences
Simon Fraser University

Address: Department of Biological Sciences
Simon Fraser Universtiy
Burnaby, British Columbia V5A 1S6
Canada

Contact(s): Michael Stanhope

Type of Research: estuarine ecology of gammarid amphipods with reference to log storage effects

Location: Squamish and Fraser River estuaries

Organization: Fisheries Research Branch,
Salmon Habitat Research Section

Address: [1]West Vancouver Laboratory,
4160 Marin eDrive,
West Vancouver, B.C. V7V 1N6
Canada

[2]Pacific Biological Station,
Departure Bay Road,
Nanaimo, B.C. V9R 5K6

Contact(s): Colin Levings[1], Michael Waldichuk[1], Mel Kotyk[1], C. McAllister[2], T.J. Brown[2], B. Kask[2], I. Birtwell[1], G. Greer[1].

Type of Research: ecology of gammarid amphipods in estuarine habitats; feeding ecology of juvenile salmonids; survivorship of chinook released in estuarine and alternate habitats; effects of domestic waste on juvenile salmonids in estuaries

Location: Fraser River, Campbell River, Nanaimo River estuaries

Organization: Pacific Biological Station

Address: Pacific Biological Station
Department of the Environment
P.O. Drawer 100
Nanaimo, British Columbia V9R 5K6
Canada

Contact(s): John Sibert, Robin LeBrasseur, Michael Healey, Brent Hargreaves

Type of Research: estuarine utilization by juvenile salmonids; ecology of epibenthic zooplankton; estuarine feeding ecology of juvenile fishes

Location: Nanaimo River estuary, other Vancouver Island estuaries

50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO.
FWS/OBS-83/05

2.

3. Recipient's Accession No.

4. Title and Subtitle
THE ECOLOGY OF ESTUARINE CHANNELS OF THE PACIFIC NORTHWEST COAST: A COMMUNITY PROFILE

5. Report Date
December 1983

6.

7. Author(s)
Charles A. Simenstad

8. Performing Organization Rept. No.

9. Performing Organization Name and Address
Fisheries Research Institute
College of Ocean and Fishery Sciences
University of Washington
Seattle, WA 98195

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
Fish and Wildlife Service
Division of Biological Services
U.S. Department of the Interior
Washington, DC 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

This report on the estuarine channel habitats of the Pacific Northwest is one of a series of community profiles that synthesize useful information about specific natural coastal habitats. This profile will assist environmental scientists and biologists and coastal planners and managers who are interested in the open-water channels of coastal estuaries from the Straits of Juan de Fuca in Washington, south to Cape Mendocino, California.

The profile describes the geomorphological, hydrological, chemical, and biological components and natural processes of the channels, their energy interchange, and interactions among adjacent habitats. In combination these habitat components and their interactions dictate the ecological structures and functions of the channels. The subject materials of the various chapters are integrated and summarized in the last chapter, and considerations for habitat management are identified.

17. Document Analysis a. Descriptors

Channels
Ecology
Pacific Northwest
Estuaries
Hydrology

b. Identifiers/Open-Ended Terms

c. COSATI Field/Group

18. Availability Statement
Unlimited

19. Security Class (This Report)
Unclassified

20. Security Class (This Page)
Unclassified

21. No. of Pages
xii + 181

22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce

☆ U.S. GOVERNMENT PRINTING OFFICE: 1984-772-308