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ECOLOGY OF ZOOPLANKTON, BENTHOS AND FISHES IN THE COLUMBIA RIVER ESTUARY

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Abstract. Fauna of the Columbia River estuary were sampled regularly for 21 months. Analyses of plankton samples indicated that three distinct populations existed in the estuary: a freshwater group, a marine group, and an indigenous estuarine group. The latter consisted principally of a large population of *Eurytemora hirundoides.* Changes in the salinity of the estuary were reflected in the composition of the plankton.

The majority of the fish and benthic invertebrates found in the estuary are euryhaline. The largest numbers of fish species, as well as the largest numbers of individuals, occupy the slightly brackish waters of the central portion of the estuary. The major plankton blooms also occur in this area. Starry flounder (*Platichthys stellatus*) and sand shrimp (*Crangon franciscorum*) use the upper estuary as a nursery ground.

Extensive analyses of fish stomach contents confirm that food habits of fishes generally reflect the availability of prey.

INTRODUCTION

The estuary of the Columbia River is an unusual and difficult habitat because of its swift currents and rapidly changing salt content. Large tidal variations combine with a great influx of fresh water to make this estuary quite unlike those on the east or gulf coasts of the United States.

The river is one of the nation's major sources of potable water. With increasing demands on this water, major changes in water levels and quality can be expected, influencing the community of animals residing in the estuary. We hope that our ecological study will serve to enumerate and identify the major animal species in the estuary before these changes occur. In a sense, it is already too late, since dams, increased silt load, altered temperatures, and other man-made changes have influenced the ecology of the river. And yet, in another sense, it is early, since at no time were oxygen levels in the estuary so low as to limit life. Compared with streams in more populous areas, the Columbia River is relatively free from pollution.

Little is known about the fauna in the estuary. Studies by the Fish Commission of Oregon (Waldron 1958; Westrheim 1955; Harry 1959) deal with ecological aspects of certain economically important species, but no work has been done on noncommercial species. Data taken by the U. S. Corps of Army Engineers (1960) concern salinity and currents in the estuary. Data of the U. S. Geological Survey (1952–1965) and U. S. Public Health Service (Robeck and Palange 1954; U. S. Public Health Service 1957–1962; 1962–1965) concern stream flow and general ecology of the river upstream from the estuary. A number of studies provide information about the ocean at the mouth of the estuary (Barnes and Paquette 1954; Aron 1962; Park, Pattullo and Wyatt 1962; Stefansson and Richards 1963; Osterberg, Pattullo and Pearcy 1964).

Physically, the estuary is large and complex.

Only a major effort, involving more manpower than was available to us, could sample the biota adequately. Thus, floral components of the ecosystem were not sampled and no study of primary production was attempted. Neither were salmonid fishes taken though they are known to migrate through the estuary where they support a significant fishery. Sampling was limited to those animals that could be collected with otter trawls, midwater trawls, and plankton nets.

This paper will deal with certain physical parameters in the estuary, a census of organisms present, food habits of the common fishes, and a few of the more obvious ecological relationships.

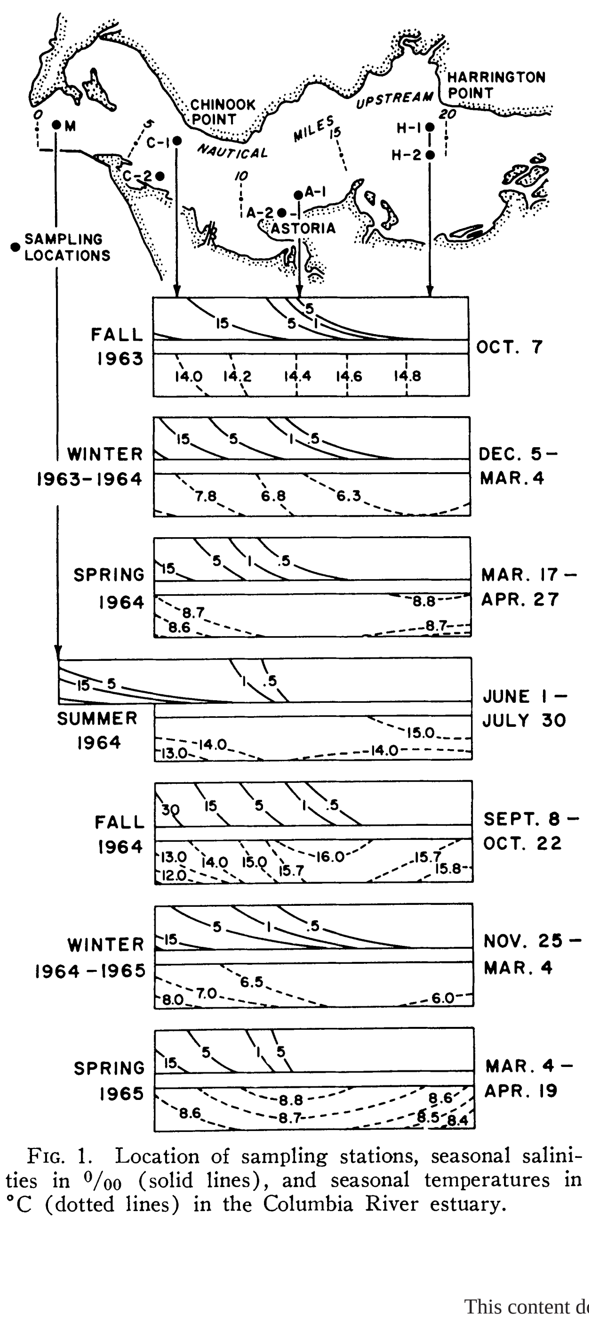

FIG. 1. Location of sampling stations, seasonal salinities in ‰ (solid lines), and seasonal temperatures in °C (dotted lines) in the Columbia River estuary.

Methods and Materials

Samples were collected monthly from 7 October 1963 to 14 July 1965 at three locations (Fig. 1): Harrington Point (H–1), Astoria (A–1), and Chinook Point (C–1). Because of channel dredging operations at the original station, a second station at Harrington Point (H–2) was added 10 June 1964, and sampled on subsequent trips. Two more stations were sampled 30 July 1964; one (M) at the mouth of the estuary, the other (C–2) opposite Chinook Point in the south channel of the estuary. Depths at the three major stations averaged around 10 m.

At each station temperatures and salinities at the surface and at the bottom were measured. Before 4 March 1964, measurements were made by CTI (conductivity-temperature-indicator). After that, a VanDorn bottle was used to collect water for salinity and oxygen determinations, and temperatures were taken with a bucket thermometer inserted into the VanDorn bottle. Oxygen content was determined by the modified Winkler method (Strickland and Parsons 1965). Turbidity was measured using a Secchi disc and water telescope.

Plankton were collected by 10-min oblique hauls with a #6-mesh half-meter net equipped with a Tsurumi-Seiki-Kosakusho recording flow meter. Samples, preserved in 10% formalin solution in the field, were analyzed by diluting the settled volume and extracting one or more cubic centimeter aliquots with a Stempel pipette until at least 100 animals were counted.

Fishes and larger invertebrates were collected in 20-min hauls, using a 22-ft (headrope length) shrimp-type otter trawl with a 1-in. mesh (stretched size). Attempts to collect benthic animals by dredging proved unsuccessful although many locations were tried. Samples were preserved in formalin and later sorted, counted, weighed, and measured. Standard fish lengths were measured. Otoliths were examined in March, June, and September 1964, and in January and April 1965. These, together with length-frequency plots were used to determine the age structure of the fish populations. Stomachs of 2,809 fish were analyzed from March 1964 to April 1965 by counting the number of each item per stomach and estimating its percentage of the total volume present. Smaller fishes and invertebrates were collected from 4 March 1965 to 14 July 1965 using a 3-ft Isaacs-Kidd midwater trawl.

Tidal fluctuations in salinity, temperature, oxygen and fauna were examined in a 25-hr study, covering a complete tidal cycle on 29–30 April 1964. Samples were taken at the Astoria station

(A–1) and on a nearby Astoria dock (A–2). On the dock, salinities and temperatures were measured every 15 min at four depths using a CTI. Salinity and oxygen were measured at surface and bottom every hour by VanDorn bottle casts. Also, a vertical plankton tow was made each hour. The midchannel station (A–1) was sampled four times, at each high and low tide. Salinity, oxygen, and temperature at the surface and the bottom were sampled by VanDorn bottle casts. Fishes and plankton were collected with 20-min otter trawl hauls and 10-min plankton tows.

Results and Discussion

Hydrography

The Columbia, largest river on the Pacific Coast, drains an area of 290,000 square miles. As much of the drainage basin is mountainous and characterized by deep winter snows, the amount of water transported by the river is high and variable. Maximum river flow averages 660,000 cfs in June and decreases between September and March to a minimum of about 70,000 cfs. Winter floods in the tributaries west of the Cascade Range may cause periods of high river flow, sometimes exceeding the June maximum (Hickson and Rodolf 1951).

Tidal variations on the Pacific Coast are large; the mean tidal range at the mouth of the river is 6.5 ft. However, tides are the mixed, semidiurnal type characterized by one of the two daily low tides being much lower, and one of the two daily high tides much higher. Thus, the mean tidal range from lower low water to higher high water is 8.5 ft.

These great variations in tides and river flow combine to create a highly dynamic environment in the Columbia estuary. An indication of the extreme variability of environmental conditions is given by the short flushing time, which Neal (1965) calculated to be between 5 and 10 days.

The maximum salinity intrusion in the Columbia occurs with high tide and low river flow and is probably less than 20 (nautical) miles, or just above the Harrington Point station. The minimum occurs with low tides and high river flow and may be less than 5 miles or just below the Chinook Point station (Neal 1965).

Seasonal salinities (Fig. 1) represent averages of measurements made on at least three sampling trips, with the exception of fall 1963 and the most seaward station for summer 1964. For these values, salinity data from only one sampling trip were available. Because of the distances between stations, it was necessary to sample different stations at different stages of the tide. Upstream records were taken at low tide and downstream records at high tide, thus encountering maximum salinities downstream and minimum salinities upstream and recording a maximum salinity gradient in the area sampled.

The salinity profile approached that of a two-layered system during periods of high river flow in summer 1964, and again in winter 1965, when flooding from heavy coastal rains occurred. Figure 1 indicates that salinities are higher in fall and winter than in spring. Probably they are not, since the lower low and high tides were sampled in the spring and summer, and the higher low and high tides were sampled in the fall and winter. This schedule was necessary so that each station would be sampled at a consistent time of day and relative stage of the tide and so that the daylight-darkness factor would not be introduced.

A 25-hr tidal cycle study was conducted in April 1964, a time of relatively low river flow. Salinity (Fig. 2) varied from 0.2‰ at the lower low tide (surface and bottom) to 19.3‰ at the higher high tide. At the higher high tide, following a net tidal range of 5.8 ft, the estuary approached a two-layered system, especially when the salt wedge initially arrived. However, at the lower high tide, following a greater net tidal range of 7.0 ft, the estuary was well mixed and surface salinities were actually greater than at the higher high tide.

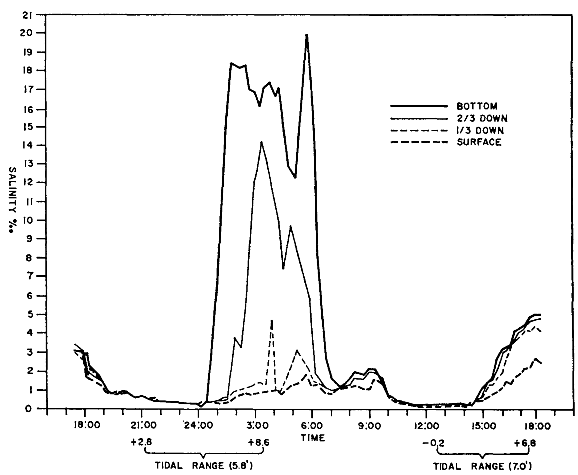

Fig. 2. Salinity (‰) at four depths during the 25-hr tidal cycle study at Astoria (A–2), April 29–30, 1964.

Seasonal temperature profiles (Fig. 1) differ from salinity profiles in shape, a result also found in the Delaware estuary by Cronin, Daiber and Hulbert (1962). Seasonal extremes are greater in the river water entering the estuary than in seawater. The river water is warmer than the salt wedge in the summer and colder in winter. Dur-

TABLE 1. Seasonal occurrence of common zooplankton measured in avg no./m³ at the station of greatest abundance. I 0.1–0.9/m³; II 1.0–9.9/m³; III 10.0–99.9/m³; IV 100.0–999.9/m³; V 1,000.0–9,999.9/m³; VI 10,000.0–99,999.0/m³

Category	Spring '64	Summer '64	Fall '64	Winter '65	Spring '65	Summer '65
Freshwater group						
Rotifera:						
Brachionus spp.	IV			II	III	II
Asplanchna sp.		III	II	III		II
Cladocera:						
Alona costata	II	III	I	II		
Chydorus globosus	II	III	III	II	II	
Diaphanosoma brachyurum		III	III			I
Ceriodaphnia quadrangula			IV			III
Bosmina spp.	IV	IV	III	II	II	IV
Daphnia longispina	III	V	III	II	II	IV
Copepoda:				II		
Diaptomus spp.	IV	III	II	III	I	III
Cyclops vernalis	IV	IV	IV	III	III	IV
Total	IV	V	V	III	III	V
Brackish group:						
Eurytemora hirundoides	VI	VI	VI	III	III	IV
Salt-intrusion group						
Cladocera:						
Evadne nordmanni		III	III			III
Copepoda:						
Acartia clausi		II	IV		III	III
A. longiremus		II	III	II	III	II
Pseudocalanus minutus		II	IV	III	IV	II
Calanus finmarchicus	III	II	II	II		
Oithona similis			III	II		
Total	III	III	IV	III	IV	IV

ing both years of this study, temperature inversion occurred during the months of November and April. Temperature extremes recorded during this study were 4.0°C on 5 January 1965 and 19.4°C on 27 July 1964.

Dissolved oxygen varied inversely with salinity and temperature. In fresh water entering the estuary, oxygen was always present in saturated or near-saturated levels. The lowest values were found in the summer-fall salt wedge, and were probably due to upwelling of oxygen-poor bottom waters offshore (Park, Pattullo, and Wyatt 1962). The lowest value measured was 2.53 ml/liter in the bottom waters at the mouth of the estuary on 30 July 1964.

Turbidity varied directly with the amount of river flow and inversely with salinity. Secchi disc readings ranged from 2.0 m at Chinook Point in September 1964 (surface salinity 29.2‰) to 0.1 m at all stations during the January 1965 flooding. However, 73% of all the Secchi disc readings were between 0.5 and 1.5 m.

Distribution of plankton

Three major planktonic groups were found, one in fresh water, one in slightly brackish water, and one in the salt intrusion (Table 1). The fresh water (0.1‰ salinity or less) plankton were dominated by a copepod *Cyclops vernalis*, and cladocerans, *Daphnia longispina* and *Bosmina* spp. Seasonally abundant species included the cladocerans *Diaphanosoma brachyurum* (summer) and *Ceriodaphnia quadrangula* (summer-fall), juvenile amphipods *Corophium salmonis* (winter-spring), the rotifers *Brachionus* spp. (spring) and *Asplanchna* spp. (summer) and copepod *Diaptomus ashlandi* (spring 1964 and summer 1965). The cladocerans *Alona costata* and *Chydorus globosus* were present in small numbers throughout the year. The highest population density recorded for the fresh water group was 2, 705/m³ at Harrington Point in late July 1964, when water temperature was highest (19.4°C) and turbidity relatively low (Secchi: 1.1 m). The population density remained high through fall and dropped to values below 100/m³ when temperatures were low (4°–8°C) and turbidity high (Secchi: 0.1–0.9 m). Although this group was most abundant at Harrington Point, the more common species often penetrated brackish waters and were collected in small numbers as far downstream as Chinook Point. These were undoubtedly carried down from upstream populations.

In slightly brackish waters the copepod *Eurytemora hirundoides* made up 90–100% of the plankton population. Few species were found in these waters but many individuals were present with population densities usually in excess of

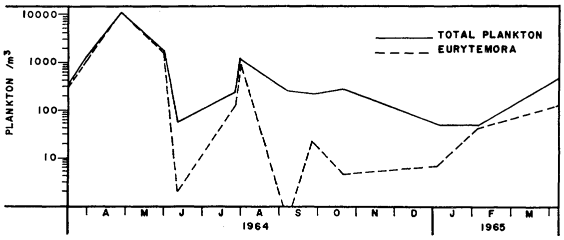

FIG. 3. Chinook Point *Eurytemora hirundoides* populations in relation to total plankton abundance.

2,500/m³. Population peaks were recorded during the course of this study in late April (108,410/m³) and late July (38,755/m³). A close relationship existed between high population density and presence of *E. hirundoides* (Fig. 3).

This species was the dominant form in the estuary and could be found at all stations. Large numbers of *E. hirundoides* were found when the surface salinity was between 0.2 and 8‰, when the mean of top and bottom salinities was between 0.2 and 16‰, and when the bottom salinity was greater than 0.2‰. These salinity limits were somewhat lower than those of Jeffries (1962a), who suggested that *Eurytemora* spp. could predominate whenever more than one-third of the length of the estuary was bounded by the 5 and 15‰ isohalines (surface). This condition was never satisfied by the Columbia during the course of this study (Fig. 1). For this population of *E. hirundoides,* Jeffries' lower boundary was much too high.

In the waters of the salt intrusion, a third group of plankton was found. Principal species were *Acartia clausi, A. longiremus,* and *Pseudocalanus minutus.* This group almost never occurred upstream of Chinook Point, and was often absent even at the mouth of the estuary during periods of high river flow. Seasonally abundant species included *Oithona similis* (fall), *Acartia tonsa* and *Corycaeus affinis* (fall 1963), and *Evadne nordmanni* (summer-fall). Analysis of stomach contents of fishes collected at Chinook Point also gave evidence of an early spring abundance of *Calanus finmarchicus* and a late summer abundance of *P. minutus.* The *Acartia-Pseudocalanus* group was found most consistently during the fall of the year when low river flow and high tides combined to create a maximum salt intrusion. High bottom salinities suggested that this group may have been present on several dates when it was not recorded. However, the waters very near the bottom could not be sampled without filling the net with sand. The highest population density recorded for this group was 755/m³ in October 1964, with values normally averaging around 500/m³.

Deevey (1956), Barlow (1955), Cronin et al. (1962), Jeffries (1962b), and Frolander (1964) found *Acartia* spp. to be much more abundant in other estuaries than in the Columbia. Many factors could have prevented the establishment of large populations in this estuary. The most obvious, however, is salinity. *Acartia* spp. are found in estuarine waters of higher salinity than that of the Columbia, where high river flow keeps salinities sufficiently low to be more favorable for *Eurytemora hirundoides.*

Maintenance of plankton populations within the estuary

Maintaining a population within an estuary is one of the most serious problems facing indigenous plankton. This problem is especially acute in an estuary with as short a flushing time (5–10 days) as the Columbia (Neal 1965). Two possible methods of maintaining a population in an estuary include achieving adequate reproductive rate to replace that portion of the plankton which is swept to sea (Ketchum 1954; Barlow 1955), and vertical and/or lateral migration of the plankton population (Cronin et al. 1962). Vertical migration would make use of the net upstream flow in the bottom waters of a two-layered system. A convenient method for determining the type of circulation system that exists has been suggested by Burt and McAlister (1959). In their method, a difference of 4‰ or more between top and bottom salinities indicates a two-layered system. *Eurytemora hirundoides* populations at stations of suitable salinity are compared (Table 2) with the type of system present, two-layered or well-mixed. No correlation was observed between the type of system and the abundance of plankton. Vertical migration was thus not shown to be a significant maintenance mechanism in Columbia *E. hirundoides* populations. Results of the 25-hr study indicated that the type of system present could vary with the stage of the tide. However, these samples were taken at approximately the same stage of the tide, just before the higher high water September through March, and just before the lower high water March through September. Tidal changes should therefore affect the data in Table 2 only on a broad seasonal basis.

Of particular interest are the plankton values on 10 June 1964 and 5 January 1965, the only sampling dates during extensive river flooding. If vertical migration were a significant mechanism, one would expect little loss of plankton populations because of the strong two-layered system present during flooding. If, however, the primary method of maintenance is reproductive

TABLE 2. Comparison of *Eurytemora hirundoides* abundance and type of estuarine circulation system present

	1964								1965					
Date and station	3/17 C-1	4/27 C-1	6/10 C-1	7/27 A-1	7/30 C-1	9/8 A-1	10/22 H-2	10/22 A-1	1/5 A-1	1/5 C-1	2/6 C-1	4/7 A-1	4/7 C-1	7/14 C-1
Top-bottom salinity difference (°/₀₀)	4	16	18	0.2	22	1	0.1	5	26	26	19	0.4	16	29
Type of system	b	b	b	a	b	a	a	b	b	b	b	a	b	b
Eurytemora (no./m³)	768	29828	5	34023	2742	5448	12910	22970	8	20	115	130	315	273

Legend: [a]well-mixed
[b]two-layered

increase, the observed reduction in numbers is expected because of the shorter flushing time during flooding. The effects of lateral migration have not been examined.

The January 1965 floods and resultant very high river flow through the estuary also provided the opportunity to observe the effects of flooding on long-term plankton maintenance. The floods apparently affected the three groups of plankton differently, although all plankton populations were low during the actual flooding.

The freshwater group was affected throughout the spring. There were two orders of magnitude less *Bosmina* spp. and *Diaptomus* spp. in spring 1965 than during the previous spring (Table 1). However, this group apparently recovered by summer 1965.

The *Eurytemora hirundoides* population was the most greatly depleted by the flooding. A difference of three orders of magnitude existed between spring 1964 and spring 1965 populations. Although some recovery was noted by summer 1965, the populations were still two orders of magnitude below those of the previous summer. Reasons for the continued lowered populations of the indigenous species are not known, but increased flushing rate during flooding may have depleted the nutrients and/or brood stock available to the plankton. Unfortunately, no nutrient data are available.

The salt wedge group suffered no aftereffects from the flood.

Distribution of benthic invertebrates

Predominant benthic species at freshwater stations (H–1, H–2) included the snail, *Hydrobia* sp., the clam, *Corbicula fluminea,* the polychaete, *Neanthes limnicola,* the oligochaete, *Enchytraeus* sp., the crayfish, *Pacifastacus trowbridgii,* the isopod, *Mesidotea entomon,* the amphipod, *Corophium salmonis,* and immature insects, especially chironomid larvae. Newly hatched sand shrimp, *Crangon* (*Crago*) *franciscorum,* were found here in early summer and were abundant through fall, but were found in more saline waters in the winter.

At Astoria (A–1), common benthic species included *M. entomon,* immature *C. franciscorum,* an amphipod *Anisogammarus confervicolus,* a harpacticoid copepod tentatively identified as *Canuella canadensis,* and a brackish water hydroid, *Cordylophora lacustris.* The number of species in this community was low probably because of the extreme salinity fluctuations (Fig. 2). Although few species were found here, individuals were often taken in great numbers, especially *Crangon franciscorum* and *Canuella canadensis.*

Major benthic species collected nearer the ocean at Chinook Point (C–1) included *C. franciscorum* (adults and immatures), the Dungeness crab *Cancer magister,* the isopod *Gnorimosphaeroma oregonensis,* and the clam *Macoma baltica.* Here, too, great salinity fluctuations may have prevented formation of a richer community.

The distribution of invertebrates by season and salinity is given in Table 3. Some species, collected only in certain seasons, were probably present throughout the year. Salinity tolerances given are conservative estimates. That is, high salinity limits of freshwater species are based on surface salinities and freshwater limits of marine species are based on bottom salinities. Species found only in the stomachs of euryhaline fish are not included in the table since salinity limits could not be determined. These included the polychaete *Hespernoe complanata,* the decapods *Callianassa californiensis* and *Scleroplax granulata,* ephemerid and heptageniid mayfly naiads, and chloroperlid stonefly naiads.

Distribution of fishes

The distribution of fishes in the estuary is greatly influenced by salinity (Table 4). Our listing of estuarine species is incomplete as only three locations were regularly sampled. Also, use of an otter trawl as the major sampling device biases the sample in favor of benthic and slow-moving fishes. As a result, anchovy and adult

TABLE 3. Distribution of invertebrates according to season and salinity

Season[b] (fresh water species)					Salinity[a]						Season (marine species)			
spring	summer	fall	winter	Classification and freshwater species	limnetic	oligohaline	mesohaline	polyhaline	euhaline	Classification and marine species	spring	summer	fall	winter
				Protozoa:										
	×	×	×	*Volvox* sp.	×									
×		×	×	*Systilus* sp.	×									
				Coelenterata:						Coelenterata:				
×		×		*Cordylophora lacustris*	×	×								
								×	×	*Aequoria* sp.			×	
								×	×	*Aurelia* sp.			×	
										Ctenophora:				
								×	×	*Pleurobrachia* sp.	×	×	×	×
				Rotifera:										
×	×			*Brachionus calyciflorus*	×	×								
×			×	*B. plicatilus*	×									
	×	×		*Asplanchna* sp.	×									
×	×	×	×	Nematoda, unidentified	×									
				Annelida:										
				Oligochaeta:										
×	×	×	×	*Enchytraeus* sp.	×									
				Polychaeta:						Polychaeta:				
×	×	×	×	*Neanthes limnicola*	×									
							×	×	×	*Neanthes brandti*	×	×		
								×	×	*Etone* sp.		×		
									×	*Goniada* sp.			×	
				Arthropoda:										
				Crustacea:						Crustacea:				
				Cladocera:						Cladocera:				
	×			*Leydigia acanthocercoides*	×									
				L. quadrangularis	×									
	×			*Monospilus dispar*	×									
	×			*Pleuroxis denticulatus*	×									
	×	×		*Ilyocryptus sordidus*	×									
	×	×	×	*Eurycercus lamellatus*	×									
		×	×	*Alona quadrangularis*	×									
	×	×		*Sida crystallina*	×	×								
	×	×		*Diaphanosoma brachyurum*	×	×								
×	×	×	×	*Alona costata*	×	×								
×	×	×	×	*Chydorus globosus*	×	×								
×		×	×	*Daphnia pulex*	×	×	×							
×	×	×	×	*D. longispina*	×	×	×							
×	×	×	×	*Bosmina*	×	×	×							
							×	×	×	*Evadne nordmanni*		×	×	
								×	×	*Podon leuckarti*		×	×	
×	×	×	×	Ostracoda, unidentified	×									
				Copepoda:						Copepoda:				
				Calanoida:						Calanoida:				
	×	×	×	*Diaptomus franciscanus*	×									
×	×		×	*D. ashlandi*	×									
×	×		×	*D. novamexicanus*	×									
×	×	×	×	*Eurytemora hirundoides*	×	×	×	×						
								×	×	*Acartia tonsa*			×	
								×	×	*A. clausi*	×	×	×	
								×	×	*A. longiremis*	×	×	×	×
								×	×	*Pseudocalanus minutus*	×	×	×	×
								×	×	*Calanus finmarchicus*	×		×	×
									×	*Paracalanus parvus*			×	
									×	*Clausocalanus arcuicornus*			×	
									×	*Centropages mcmurrichi*			×	
				Cyclopoida:						Cyclopoida:				
		×	×	*Paracyclops fimbriatus*	×									
×	×	×	×	*Cyclops vernalis*	×	×	×	×						
								×	×	*Oithona similis*	×		×	×
								×	×	*Corycaeus affinis*			×	×
				Harpacticoida:						Harpacticoida:				
×				*Bryocamptus hiemalis*	×									
						×	×	×		*Canuella canadensis*	×	×	×	×

TABLE 3.—Continued

Season[b] (fresh water species): spring	summer	fall	winter	Classification and freshwater species	Salinity[a]: limnetic	oligohaline	mesohaline	polyhaline	euhaline	Classification and marine species	Season (marine species): spring	summer	fall	winter
								×	×	Cirripedia, unid. larvae	×		×	×
										Nebaliaceae:				
									×	*Epinebalia pugettensis*		×		
				Mysidaceae:						Mysidaceae:				
×	×	×	×	*Neomysis mercedis*	×	×	×							
							×	×	×	*Neomysis kadiakensis*	×	×	×	×
								×	×	*N. rayii*	×			×
									×	*Acanthomysis macropsis*	×	×		
									×	*Archaeomysis grebnitzkii*	×	×	×	×
										Euphausiaceae:				
									×	*Thysanoessa longipes*		×		×
				Amphipoda:						Amphipoda:				
										Hyperidae, unidentified		×	×	
				Gammaridae:						Gammaridae:				
×	×	×	×	*Corophium salmonis*	×	×								
							×	×	×	*Corophium spinicorne*	×		×	×
					×	×	×	×	×	*Anisogammarus confervicolus*	×	×	×	×
								×	×	*Paraphoxius milleri*	×	×	×	×
									×	*Jassa falcata*		×		
				Isopoda:						Isopoda:				
			×	*Asellus* sp.	×									
×	×	×	×	*Mesidotea entomon*	×	×	×							
							×	×	×	*Gnorimosphaeroma oregonensis*	×	×	×	×
				Decapoda:						Decapoda:				
×	×	×	×	*Pacifastacus trowbridgii*	×									
					×	×	×	×	×	*Crangon franciscorum*	×	×	×	×
									×	*C. nigricauda*		×	×	×
							×	×	×	*Cancer magister*	×	×	×	×
				Insecta:										
	×		×	Ephemerillidae	×									
	×			Gerridae	×									
×				Plecoptera, unidentified	×									
			×	Perlodidae	×									
×	×	×	×	Chironomidae	×	×								
				Arachnida:										
			×	Hydracarina, unidentified	×									
				Mollusca:						Mollusca:				
				Gastropoda:						Gastropoda:				
×	×	×	×	*Hydrobia* sp.	×									
	×			*Pleurocera* sp.	×									
									×	*Nassarius* sp.		×		
				Pelecypoda:						Pelecypoda:				
×	×	×	×	*Anadonta* sp.	×									
×	×	×	×	*Corbicula fluminea*	×									
							×	×		*Macoma baltica*	×	×	×	×

[a]Limnetic 0–0.5%, oligohaline 0.5–5%, mesohaline 5–18%, polyhaline 18–30%, euhaline 30%.
[b]Spring 3/4–4/30, summer 6/1–7/30, fall 9/8–11/5, winter 11/22–3/4

salmonids, though known to be present, were not sampled.

The bulk of the catch at all stations was made up of euryhaline species. In this group, the most common were the starry flounder (*Platichthys stellatus*), prickly sculpin (*Cottus asper*), staghorn sculpin (*Leptocottus armatus*), longfin smelt (*Spirinchus dilatus*), Pacific tomcod (*Microgadus proximus*), and Pacific snakeblenny (*Lumpenus sagitta*). Of these, only *C. asper* is a freshwater species.

Large numbers of very young flounder (*P. stellatus*), 0–1 year classes, were normally caught upstream in fresh water, but were infrequent in waters of high salinity (Fig. 4). *P. stellatus* older than 2½ yr were seldom caught in the estuary. Whether this was due to emigration, mortality, or ability to evade the trawls is not known. It is likely that this species used the upper estuary as a nursery ground for its young. Many authors have reported use of estuaries as nursery grounds in pleuronectid and other fishes

TABLE 4. Fish species collected at all stations in otter and midwater trawls with estimate of salinity distribution

Species		Fresh water 0–0.5	Oligo-haline 0.5–5	Meso-haline 5–18	Poly-haline 18–30	Marine >30
Peamouth	*Mylocheilus caurinus*	*				
Largescale sucker	*Catostomus macrocheilus*	*				
Riffle sculpin	*Cottus gulosis*	*				
White sturgeon	*Acipenser transmontanus*	*				
Threespine stickleback	*Gasterosteus aculeatus*	*				
Prickly sculpin	*Cottus asper*	*	*	*		
Starry flounder	*Platichthys stellatus*	*	*	*	*	*
Pacific staghorn sculpin	*Leptocottus armatus*	*	*	*	*	*
Longfin smelt	*Spirinchus dilatus*	*	*	*	*	*
Eulachon	*Thaleichthys pacificus*	*	*	*	*	*
Surf smelt	*Hypomesus pretiosus*	*	*	*	*	*
American shad	*Alosa sapidissima*	*	*	*	*	*
Chinook salmon	*Onchorhynchos tschawytscha*	*	*	*	*	*
Pacific lamprey	*Lampetra tridentata*	*	*	*	*	*
Pacific tomcod	*Microgadus proximus*		*	*	*	*
Pacific snakeblenny	*Lumpenus sagitta*		*	*	*	*
Shiner perch	*Cymatogaster aggregata*		*	*	*	*
Sand sole	*Psettichthys melanostictus*			*	*	*
Showy snailfish	*Liparis pulchellis*			*	*	*
Northern anchovy	*Engraulis mordax*				*	*
Lemon sole	*Parophrys vetula*				*	*
Whitebait smelt	*Allosmerus elongatus*					*
Arctic smelt	*Osmerus dentex*					*
Pacific sand lance	*Ammodytes hexapterus*					*
Blacktip poacher	*Xeneretmus latifrons*					*
Buffalo sculpin	*Enophrys bison*					*
Pacific sandfish	*Trichodon trichodon*					*
Spiny dogfish	*Squalus acanthias*					*
Longnose skate	*Raja rhina*					*
Pacific hake	*Merluccius productus*					*
Blackmouth rockfish	*Sebastodes crameri*					*

(Orcutt 1950; Ketchen 1956, Gunter 1957; Pearcy 1962).

The greatest variety and number of fishes were taken consistently in water of oligohaline to mesohaline salinities (0.5 to $18^{0}/_{00}$ according to the Venice system, anonymous 1958). This was true whether these waters were found at the Astoria station, as they were in the fall of both years, or the Chinook Point station, as in the other seasons (Fig. 5). These stations were usually also the sites of the large blooms of *E. hirundoides* at those times.

The 25-hr study in April 1964 (station A–1) showed that freshwater species were present during lower tides only, and marine-brackish species during higher tides only. Euryhaline species were present at all stages of the tide.

Food habits of the fishes

Although most of the fish species examined consumed wide varieties of prey, the bulk of the food usually comprised only a few species. Most amphipods consumed in fresh water were *Corophium salmonis,* and in brackish to marine waters, *Archaeomysis grebnitzkii.* Most of the copepods consumed in fresh water were *Cyclops vernalis;* in brackish to marine water they were *Eurytemora hirundoides* and *Calanus finmarchicus.* In water of all salinities, the sand shrimp, *Crangon franciscorum,* was the most common decapod eaten. Rapid digestion made identification of polychaetes difficult, and as a result, few were recorded. However, it is probably safe to assume that most of the polychaetes taken in fresh water were *Neanthes limnicola.* In all salinities, the longfin smelt (*S. dilatus*) was the most common fish consumed.

Relative abundance of prey species in fish stomachs coincided with the relative abundance of these species in midwater trawls and plankton tows. Exceptions included *Neanthes limnicola, Corophium salmonis,* and *Archaeomysis grebnitzkii.* The choice of sampling methods may have accounted for the larger relative abundance of the first two species in fish stomachs since both are too small to be captured by the otter trawl and too benthic to be taken by usual plankton tows and midwater trawls. Why *A. grebnitzkii* was the most abundant mysid in fish stomachs of marine to brackish waters is not known. Midwater trawls were successful in capturing both large numbers of other mysid species and some of the fish predators, but *A. grebnitzkii* itself was almost never taken, suggesting that it may also be benthic in habitat.

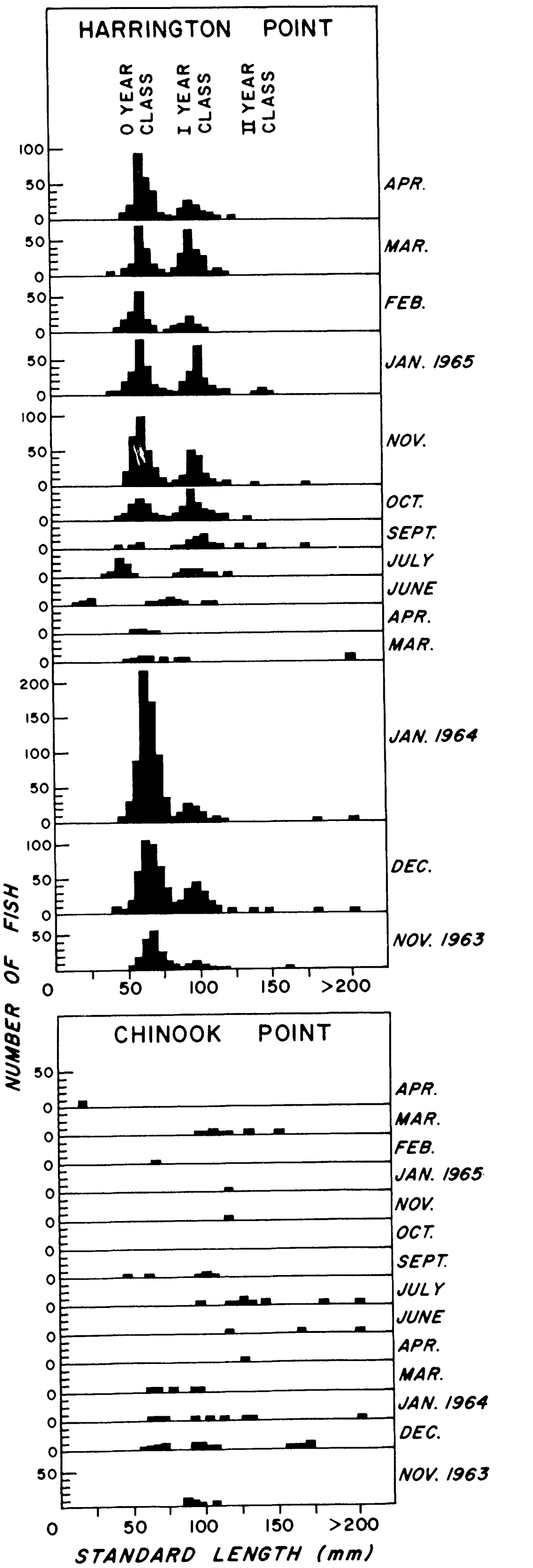

FIG. 4. Monthly length-frequency curves of starry flounder *Platichthys stellatus* at Harrington Point (fresh water) and Chinook Point (brackish to marine water) stations.

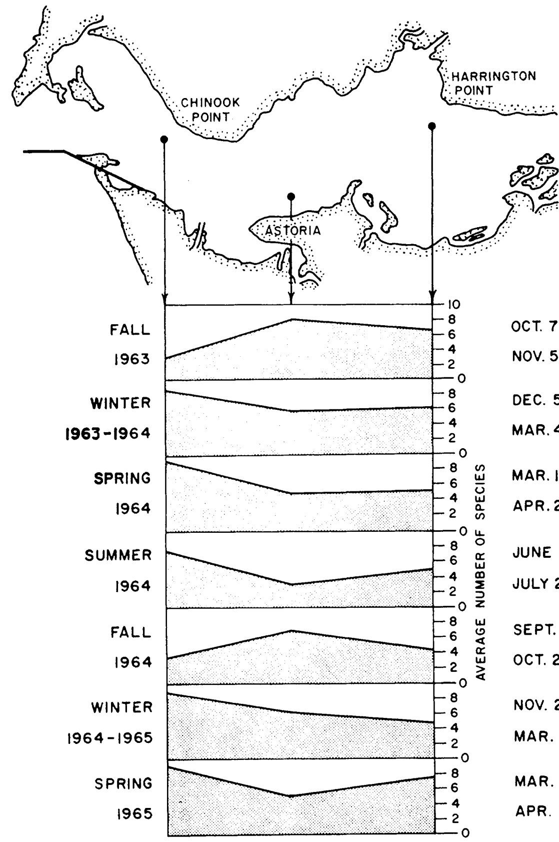

FIG. 5. Seasonal average numbers of species of fish taken at major stations in the Columbia River estuary.

Four major types of food habits are noted in the common fish species examined (Fig. 6). Fishes in group I: snakeblennies (*L. sagitta*), smelt (*S. dilatus*), and very young flounder (*P. stellatus*), are plankton feeders that eat large quantities of copepods. Fishes in group II: larger juvenile *P. stellatus,* prickly sculpin (*C. asper*), and young sturgeon (*Acipensor transmontanus*) are primarily bottom feeders that eat mostly amphipods and polychaetes. Fishes in group IV: older staghorn sculpin (*L. armatus*) and sand sole (*Psettichthys melanostictus*), consume primarily fish. Fishes in group III: younger *L. armatus,* young lemon sole (*Parophrys vetula*), and tomcod (*M. proximus*), eat all types of food.

Smelt (*S. dilatus*), prickly sculpin (*C. asper*), and snakeblenny (*L. sagitta*), showed no major changes in food habits with increasing age or size. Gradual dietary changes with age were noted in tomcod (*M. proximus*) and staghorn sculpin (*L. armatus*). In both cases the diet changed from smaller (copepods and amphipods) to larger prey (fish and decapods). A striking change involved 0-year-class flounder (*P. stellatus*), which, after reaching a length of 50–60 mm, shifted their diet

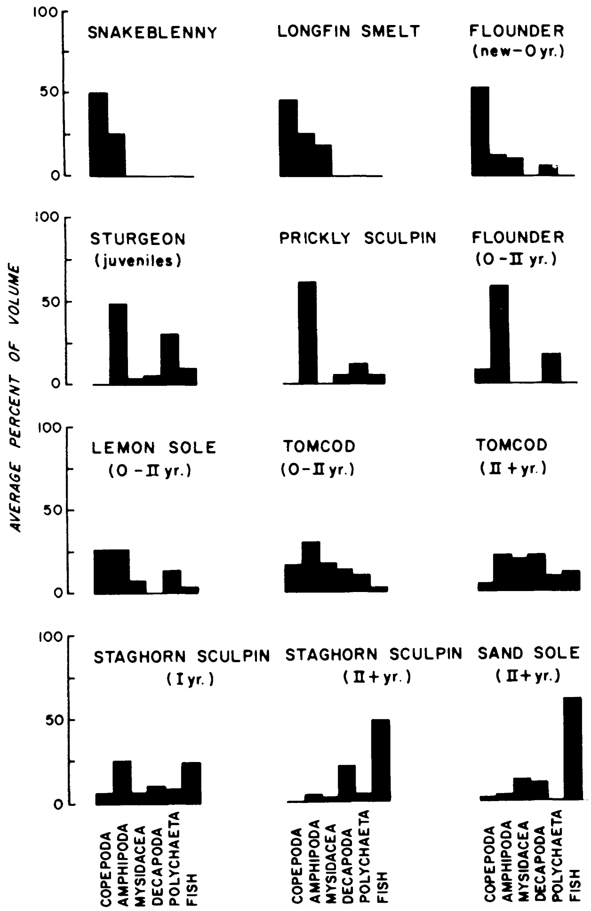

FIG. 6. Stomach contents of various fishes in the Columbia River estuary.

from copepods to amphipods. This was also noted by Orcutt (1950).

Pronounced seasonal differences occur in the diet of most fishes, often because of the availability of prey species. For example, during the high, late-spring plankton populations of 1964, the copepod *Eurytemora hirundoides* made up a large part of the plankton and of the diet of many fish which do not eat copepods at other seasons. Flounder (*P. stellatus*) and tomcod (*M. proximus*) (Table 5) fed on this species in spring 1964 but not in spring 1965, undoubtedly because the *E. hirundoides* populations were much lower (Table 1).

Some unexpected food changes were noted in winter. Lemon sole (*P. vetula*) consumed large quantities of sipunculate worms during February and March, a drastic departure from their usual winter starvation diet. Also, sculpins (*L. armatus* and *C. asper*) and tomcod (*M. proximus*) consumed larger percentages of polychaetes during the winter months (Table 5). As polychaetes were presumably present throughout the year, this may have been because of scarcity of other foods.

Some seasonal dietary changes resulted when large numbers of the young of prey species occurred. These young were apparently quite abundant and/or easy to obtain. One of the most vivid examples of this involved the young of the sand shrimp *Crangon franciscorum* which were abundant in stomachs of sculpin (*C. asper*) from fresh water at about the same time that the young shrimp first appeared in fresh water (early summer). Young shrimp were taken in much greater numbers in otter trawls in the fall of the year than in early summer, but *C. asper* consumed fewer shrimp in the fall (Table 5). However, the discrepancy between abundance of shrimp in the otter trawls and fish stomachs is not necessarily significant since early summer shrimp were smaller and could more easily pass through the otter trawl mesh.

Other young utilized as food included megalops and the very young of Dungeness crab (*Cancer magister*) eaten in summer by tomcod (*M. proximus*), and very young clams, *Corbicula fluminea*, eaten in summer by flounder (*P. stellatus*) at Harrington Point.

All seasonal differences may not have depended upon the availability of food. For example, about 50% of the diet of both flounder (*P. stellatus*) and sculpin (*C. asper*) consisted of the amphipod *Corophium salmonis*. However, food consumption in *P. stellatus* all but stopped during the winter when 90% of the stomachs were empty: note that growth also stopped during the winter (Fig. 4)—whereas *C. asper* continued to eat (Table 6). *C. asper* consumed peak numbers of *C. salmonis* during the spring of the year when the amphipod was most abundant in the plankton, but *P. stellatus* consumed most during the summer and the fall.

Many fish species were sufficiently euryhaline to be collected in waters of more than one salinity. It was virtually impossible to compare fish food habits in different salinities, because many of the invertebrate species were less likely to move in and out with the changes in salinities than were their fish predators. As a result, food habit changes caused by differences in salinity were difficult to distinguish from those caused by difference in location. Furthermore, the seasonal abundance of a prey species at one location often did not correspond to the seasonal abundance of a similar type of prey at a different location. Thus, not only the specific composition, but also the major types of food in the diet of a fish species could vary greatly depending on station and season.

TABLE 5. Seasonal food preferences of three common fish species

Fish species and age group	Category	Season: Spring 1964	Summer 1964	Fall 1964	Winter 1964	Spring 1965
Platichthys stellatus	Station	A	H	H	H	H
0.5-2.5 yr	Number of fish examined	65	48	124	176	126
	Major food items (% volume)					
	Polychaeta	0	17	15	21	29
	Eurytemora hirundoides	66	0	0	0	0
	Corophium salmonis	25	58	77	72	34
	Corbicula fluminea	0	21	4	0	0
	Per cent empty stomachs	51	29	22	90	44
Cottus asper	Station	A	HA	HA	HA	HA
all ages	Number of fish examined	14	54	58	111	101
	Major food items (% volume)					
	Polychaeta	0	2	15	20	5
	Corophium salmonis	42	38	57	34	82
	Anisogammarus sp.	17	5	2	9	5
	Mesidotea entomon	16	2	4	0	1
	Crangon franciscorum	0	20	5	0	0
	Lampetra tridentata	8	+	0	2	2
	Per cent empty stomachs	0	11	7	12	1
Microgadus proximus	Station	C	C	C	C	C
all ages	Number of fish examined	34	125	34	66	26
	Major food items (% volume)					
	Polychaeta		2	5	16	5
	Eurytemora hirundoides	++	20	0	0	0
	Calanus finmarchicus	++	0	0	0	33
	Anisogammarus sp.	++	31	1	9	12
	Archaeomysis grebnitzkii	++	10	37	34	16
	Crangon sp.		11	14	2	0
	Cancer magister		6	2	1	0
	Fish		6	19	10	6
	Per cent empty stomachs		0	3	0	0

+=present in trace amounts ++=abundant but % volume not determined

TABLE 6. Seasonal consumption of *Corophium salmonis* by prickly sculpin and starry flounder

Category	Spring 1964 (A-1)	Summer 1964 (H-2)	Fall 1964 (H-2)	Winter 1964 (H-2)	Spring 1965 (H-2)
No. fish examined:					
Sculpin (all ages)	14	54	58	111	101
Flounder (0 and 1 yr)	65	48	124	174	126
Corophium salmonis (avg No./fish):					
Sculpin (all ages)	19.7	7.8	8.9	3.5	21.9
Flounder (0 and 1 yr)	1.3	2.9	3.6	<0.1	1.0
Percent empty stomachs:					
Sculpin (all ages)	0	11	7	12	1
Flounder (0 and 1 yr)	51	29	22	90	44

Since differences in food habits with season and salinity often reflected availability of food, the life histories of prey species were undoubtedly controlling factors. Further investigation, especially of the distribution, life cycles, and abundance of prey species, is necessary adequately to describe the existing complex relationships.

Distribution of abundance and diversity

It is generally assumed that the number of species in an estuary increases as one progresses seaward (Hedgpeth 1957; Frolander 1964) and that the population in any area of environmental extremes tends to contain few species and many individuals (Segerstrale 1949). In the Columbia River estuary other factors tend to complicate the picture. The plankton of the "environmental extreme" of the slightly brackish waters is almost exclusively the copepod *Eurytemora hirundoides* which occurs in tremendous numbers. The number of predator fishes associated with this excellent food source increases so that many more species (Fig. 5) and individuals are represented in the slightly brackish waters of this "environmental extreme" than in more saline and presumably less hostile waters seaward. Consequently, the fishes appear to be less numerous and varied in the seaward "favorable" habitat, whereas the plankton behave in the more traditional manner. One can conclude only that an environmental extreme which limits the number of species to a few with many individuals may be modified by the presence of those few species to become a favorable environment for another group of species.

Conclusions

The large Pacific Coast tidal range and great variations in Columbia River flow combine to make the Columbia estuary a diverse and rapidly changing environment. As a result, most of the organisms present in the estuary are euryhaline. True freshwater species may penetrate far downstream at times of high river flow and low tidal range, undoubtedly because the surface waters remain fresh. At the same time and in the same location, true marine species may be found in the saline bottom waters. This distribution is unstable even though high river flow favors a two-layered system. The high tidal range works against stability by providing energy for mixing. As a result, the two-layered system is only maintained for portions of the tidal cycle.

Three major plankton groups are found in the estuary: those that migrate or are carried in from fresh water and generally remain associated with the freshwater masses in the estuary, those that enter the estuary from the ocean and generally remain associated with the salt waters of the estuary, and those that are indigenous to the estuary and are associated with slightly brackish waters. The indigenous, brackish water group is characterized by much larger numbers of individuals and smaller numbers of species than the adjacent fresh water or marine groups. Changes in the salinity of the estuary are reflected in the composition of the plankton.

Floods during January 1965 affected the three planktonic groups differently. The fresh water group was greatly decreased in numbers but recovered rapidly. The marine group was not affected. The estuarine group was reduced by three orders of magnitude and recovered slowly.

Fish appear to be most abundant in the slightly brackish waters characterized by high plankton populations. Fish populations differ from plankton populations in that larger numbers of species as well as larger numbers of individuals are found in these waters.

At least two marine species may be using the relatively fresh, upper estuary as a nursery ground for their young. Juvenile starry flounder (*Platichthys stellatus*) appear to remain in the upper estuary until they are 2–2½ yr old. Juvenile sand shrimp (*Crangon franciscorum*) remain only one season, arriving in fresh water in June or July and leaving in November or December.

Stomach analyses show a variety of food habits in the fishes examined. Fish species can be roughly divided into those feeding on plankton, those feeding on benthos, those feeding on other fishes, and those feeding on combinations of plankton, benthos, and fish. Although most fish consume many prey species, the bulk of their food is made up of only a few species. Availability of the prey species probably determines differences in food habits with season and salinity.

Acknowledgments

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EFFECTS OF PHYSICAL-CHEMICAL FACTORS ON THE DISTRIBUTION AND OCCURRENCE OF SOME SOUTHEASTERN WYOMING PHYLLOPODS

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Abstract. Field and laboratory evidence demonstrates that differences in tolerance to salinity and temperature of phyllopods notably affect their habitat types and seasonal occurrence. Oxygen concentration and pH are of lesser ecological consequence. The 11 phyllopods studied are categorized according to their seasonal occurrence and habitat salinities. For example, based on the tolerance of both eggs and adults, *Branchinecta lindahli* is eurythermal and euryhaline, whereas *Triops longicaudatus* is stenothermal and stenohaline. Though some adult phyllopods endure substantial ranges in salinity and temperature, their eggs are not necessarily so adapted. In some instances egg hatchability is impeded by environments not hostile to adult shrimp. Phyllopod eggs are, therefore, instrumental in defining when and where a particular species occurs. Ephemeral ponds with moderately high magnesium concentrations may be hostile to some phyllopods.

Although considerable work has been done on various aspects of phyllopod biology, little is known of the influence of physical-chemical factors on their distribution and occurrence in ephemeral ponds. Animals inhabiting temporary ponds are frequently subjected to extreme and rapid fluctuations in such environmental factors as salinity and temperature. For example, alpine phyllopods tolerate water temperatures that are often near freezing and osmotic concentrations that are similar to that of distilled water, whereas most other species are inhabitants of periodic prairie and desert ponds where evaporation rates are high. In such situations rapid fluctuations in salinity are frequent, and temperatures occasionally extreme.

Aside from the general scarcity of information

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