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March 1986

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ABSTRACT

The diets of 25 fish species collected in demersal, pelagic, and intertidal habitats of the Columbia River estuary (Washington and Oregon) were studied from February 1980 through January 1981. Distinct feeding guilds (fishes with similar diets) were identifiable in every season. Guilds were represented by more species in spring and summer because of the presence of anadromous species and probably also in response to abundant prey. Some fishes showed large seasonal variations in diet. The kinds of prey consumed appeared to be determined by their seasonal abundances and availability. The limited food resource partitioning indicates little competition and may be a result of abundant but species-poor prey resources. Widely fluctuating estuarine physical conditions may also play an important role.

Introduction

Pacific coast estuaries are important for many recreationally and commercially valuable fishes (Healey 1982; Simenstad et al. 1982). The Columbia River estuary (Washington and Oregon) is one of the largest on the Pacific coast of North America, covering 37,230 ha (92,000 acres). Principal sport and commercial fishes that feed in the estuary during at least part of their life include white sturgeon, Acipenser transmontanus; American shad, Alosa sapidissima; cutthroat trout, Salmo clarki; steelhead, S. gairdneri; and four species of Pacific salmon, Oncorhynchus spp.

Previous information on food of Columbia River estuarine fishes was presented by Haertel and Osterberg (1967) for trawl-caught fishes and McCabe et al. (1983) for fishes commonly caught together with salmonids. Our paper adds to their work by including fishes collected from three gear types over a full year.

The estuarine feeding habits of some of the fish species in this paper have been studied (Turner and Kelley 1966; Conley 1977; Levy and Levings 1978), but few authors have attempted to present fish feeding patterns of an entire ecosystem. By identifying the feeding habits of fishes of an entire ecosystem, potential competition, predation, and other interspecific relationships can be determined (Tyler 1972; Langton and Bowman 1980).

The primary objective of our study was to describe spatial and temporal variations in the food of fishes in the Columbia River estuary on an assemblage level. In addition, we present food data for some fish species for which there is little published information.

Methods

Sampling

Estuarine habitats were sampled with a bottom trawl, a purse seine, and beach seines. Demersal habitats were sampled with an 8-m semiballoon shrimp trawl that had an overall mesh size (stretched) of 38.1 mm; a knotless 12.7 mm (stretched) liner was inserted in the net's cod end. Pelagic areas were sampled with a 200-m by 9.8-m variable mesh purse seine. Mesh sizes (stretched) in the seine included 19.0 and 12.7 mm. Intertidal areas (and sometimes adjacent subtidal areas) were sampled with two 50-m beach seines that were 4.0 m and 3.4 m deep at their deepest points. Both nets contained the following mesh sizes (stretched): 19.0 mm, 12.7 mm, and 9.5 mm.

Sampling was conducted monthly at 22 demersal sites, 16 pelagic sites, and 11 intertidal sites (Fig. 1). Fish sampling began in February 1980 and ended in July 1981; fish feeding data were collected from February 1980 through January 1981. Due to time and funding constraints, feeding samples taken from February through July 1981 were not analyzed.

If available, a subsample of five individuals of each species (and age group for chinook salmon, O. tshawytscha) for each sampling effort was selected for stomach analysis. Selected fish were injected immediately after capture with a buffered 8% formaldehyde solution to preserve the fish and to prevent continued digestion of stomach contents (Emmett et al. 1982). In the laboratory, injected fish were weighed to the nearest gram and measured to the nearest millimeter, and their stomachs were removed and stored in vials containing a 70% ethyl alcohol solution. Fish stomach contents were examined using a 10X binocular microscope. Prey items were identified to the lowest practical taxon and counted. Each prey taxon was weighed to the nearest 0.1 mg after being blotted and air dried for 10 min.

Although we attempted to identify the food of all Columbia River estuarine fishes, we were limited in manpower and sample size. This paper is based on 25 fish species that had sufficient sample size to allow adequate description of their diet. A list of the fishes analyzed with sample size is shown in Table 1. When possible, predators were sorted into age classes using length frequency distributions.

Data Analysis

The diet for each species was described using an Index of Relative Importance (IRI) modified from Pinkas et al. (1971):

$$IRI = \%F_n\ (\%N_n + \%W_n)$$

where: $\%F_n$ = frequency of occurrence of prey item "n" eaten by a predator

$\%N_n$ = percent number of prey "n" eaten by a predator

$\%W_n$ = percent weight of prey "n" eaten by a predator.

To more easily identify primary prey items, IRI values for each fish species were converted to percentages.

To identify feeding guilds (groups of species which consume similar prey), diet overlap values were calculated using a modification of Morisita's (1959) formula (Horn 1966):

$$C = \frac{2\sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where: C = overlap coefficient

s = food categories

X_i = percent IRI of food category i in fish species X

Y_i = percent IRI of food category i in fish species Y.

Percent IRI values were used in the overlap formula since we felt these values best represented the diets of fishes. Overlap values greater than or equal to 0.6 were considered significant (Zaret and Rand 1971), and the compared species were considered part of a guild.

Food data were analyzed by season: spring (April-June), summer (July-September), fall (October-December), and winter (January-March).

Results

Fishes of the Columbia River estuary consumed a large variety of prey. Although six phyla ranging from Nemertea to Chordata were represented, the most frequent prey were crustaceans.

Spring

Four feeding guilds were identified in spring in the Columbia River estuary (Fig. 2). Guild 1 was composed of demersal and pelagic plankton feeders that consumed calanoid copepods as primary prey (Fig. 3). Guild 2 consisted of demersal, pelagic, and intertidal fishes that consumed primarily the gammarid amphipod *Corophium salmonis*. Guild 3 was composed of two marine demersal epibenthos feeders that consumed the mysid *Archaeomysis* grebnitzkii. Guild 4 consisted of two demersal fishes that preyed heavily on the epibenthic amphipods, Eogammarus spp.

Summer

In summer, some fish, such as age 0 chinook salmon and Pacific herring, Clupea harengus pallasi, switched from their spring prey. Four feeding guilds were identifiable, although the first two did not have a distinct separation (Fig. 4). The first guild (pelagic and intertidal plankton feeders) consumed primarily cladocerans, Daphnia spp., although calanoid copepods were also important (Fig. 5). The second guild (primarily pelagic plankton feeders) fed chiefly on calanoid copepods, with Daphnia spp. secondarily important. The third guild (pelagic and intertidal epibenthos feeders) ate chiefly harpacticoid copepods. The fourth guild was composed primarily of demersal fishes that preyed on Corophium salmonis.

Fall

In fall, three guilds were identified (Fig. 6). Pacific herring (age class 0) and longfin smelt, Spirinchus thaleichthys (age class 0 and 1) comprised a pelagic plankton feeding guild that ate chiefly calanoid copepods (Fig. 7). The second guild, composed of demersal epibenthos feeders, Pacific tomcod, Microgadus proximus, and Pacific staghorn sculpin, Leptocottus armatus, concentrated their feeding on the shrimp Crangon franciscorum. A demersal-intertidal benthos feeding guild was composed of prickly sculpin, Cottus asper, and age group 0 and 1 starry flounder, Platichthys stellatus, preying primarily on Corophium salmonis. Subyearling chinook salmon and English sole, Parophrys vetulus, had little or no diet overlap with other species.

Winter

In winter, three feeding guilds were identified (Fig. 8). The first guild, pelagic plankton feeders, consisted of American shad (age group 1), Pacific herring (age group 1), and surf smelt, *Hypomesus pretiosus*; these fishes concentrated their feeding on calanoid copepods (Fig. 9). The second guild included pelagic, demersal, and intertidal fishes that fed chiefly on *C. salmonis.* The third guild was composed of two demersal epibenthos feeders, Pacific tomcod and English sole (age class 0), that preyed primarily on *Eogammarus* spp.

General Results

This study indicated that: 1) feeding guilds were common in the Columbia River estuary, 2) relatively few prey taxa were consumed in quantity, and 3) seasonal shifts occurred in the diets of many fishes. In order of importance, *Corophium salmonis,* calanoid copepods (mostly *Eurytemora affinis*), *Daphnia* spp., harpacticoid copepods (mostly *Scottolana canadensis*), *Neomysis mercedis, Crangon franciscorum, Archaeomysis grebnitzkii,* and *Eogammarus* spp. were the primary prey for most Columbia River estuarine fishes. Their importance was dependent upon habitat and season. For example, *C. salmonis* was the primary prey for many pelagic fishes in spring, but not in summer when many fishes switched to *Daphnia* spp. *Corophium salmonis* was consumed by many fish in the pelagic habitats only in winter and spring. In intertidal and demersal habitats, *C. salmonis* was consumed year round.

Discussion

The level of prey identification can affect the overlap values (Langton and Bowman 1980). The use of general taxonomic groupings usually increases overlap values, whereas using specific taxonomic identifications may reduce values. Diet overlaps might have been lower if all prey had been identified to species. Also, sample size can affect the overlap values if it is not large enough to accurately describe the diet (Hoffman 1978). The smaller the sample size, the more variable the diet overlap. We attempted to analyze as many stomachs from as many fish species as was feasible. Lastly, biological factors related to the time of collection may influence fish food studies. Some fishes have diel feeding habits (Godin 1981), whereas others are affected by tidal stage (Congleton 1978). It is possible that we did not collect all fishes during their optimum feeding times. A series of diel fish collections was made, but funding constraints prevented an analysis.

Haertel and Osterberg (1967) identified four feeding groups in trawled fish from the Columbia River estuary: plankton eaters, benthos eaters, combination eaters, and fish eaters. Although we found that some fishes consumed fish, we did not identify a fish feeding guild. We found that most fishes in the Columbia River estuary were feeding in identifiable guilds. Feeding guilds were more obvious in spring and summer and less obvious in fall and winter. This may be a result of the number of species analyzed--fewer fish were captured in fall and winter and fewer stomachs were analyzed from those seasons. The fewer guilds may also have resulted from lower prey concentrations causing fish to direct their feeding toward prey items that they were morphologically best adapted to prey upon (Zaret and

Rand 1971); thus a large number of fish species in fall and winter would not have high diet overlaps.

The gammarid amphipod *Corophium salmonis* was a major prey for many of the guilds, especially in spring. The prevalence of *C. salmonis* in the diets of many fishes may be a result of two factors. First, *C. salmonis* is an abundant macrobenthic invertebrate in the Columbia River estuary (Holton et al. 1984; Wilson 1983). Second, we speculate that *C. salmonis* diel behavior (Davis 1978), catastrophic drift (Waters 1965), and possibly migratory behavior (Wilson 1983) cause large numbers of *C. salmonis* to be swept into the water column where they are selected by fishes because of their large size relative to other plankton. Supporting this hypothesis is the fact that *C. salmonis* was primary prey for many fishes (even pelagic feeders) in spring, when river flows are high; but not in summer, when river flows are low (Neal 1972). Intertidal and demersal fishes, such as starry flounder and prickly sculpin, feed on *C. salmonis* throughout the year because they feed on the bottom where *C. salmonis* live in tubes.

In other Pacific coast estuaries, the mysid *Neomysis mercedis* is a primary prey for many fishes (Levy and Levings 1978). *N. mercedis* is the most abundant mysid in the Columbia River estuary (Williams 1983), but was primary prey for only a few demersal and intertidal fishes.

The importance of *Daphnia* spp. as prey in summer was probably related to their estuarine abundance at this time. Haertel and Osterberg (1967) observed that freshwater plankton (*Daphnia* spp. and others) reached their greatest abundance in the Columbia River estuary in summer and fall. *Daphnia* spp. are probably preferred prey for many fishes because they are large and non-evasive (Eggers 1982). Craddock et al. (1976) found that subyearling chinook salmon actively selected *Daphnia* spp. over other zooplankton during summer in the lower Columbia River.

Large numbers of pelagic schooling fishes such as American shad; Pacific herring; northern anchovy, *Engraulis mordax*; surf smelt; and longfin smelt fed primarily on calanoid copepods. Other fishes that preyed primarily on calanoid copepods were chum salmon, *O. keta*; sockeye salmon, *O. nerka*; threespine stickleback, *Gasterosteus aculeatus*; and Pacific sand lance, *Ammodytes hexapterus*. The middle of the Columbia River estuary (River Kilometer 5 to 21) has tremendous numbers of calanoid copepods, with *Eurytemora affinis* comprising 90-100% of their numbers (Haertel and Osterberg 1967). Probably as a result, the highest densities of fishes that fed on calanoid copepods occurred in this area in spring and summer (Bottom et al. 1984) when *E. affinis* normally have their peak densities (Haertel and Osterberg 1967).

The high diet overlaps that occurred among many of the fishes in the Columbia River estuary do not necessarily indicate competition. Competition occurs only if a resource, such as food, is limiting (Zaret and Rand 1971; Keast 1978). When food becomes limiting or is less abundant, fish become specialized feeders (preying on species for which they have the best-adapted behavior, digestive morphology, and mouth structure) (Macdonald and Green 1986); but when a particular prey is extremely abundant, fish feed upon that prey (Nilsson 1967; Zaret and Rand 1971; Keast 1978; MacPherson 1981). Under variable conditions where populations or communities are not in a resource-defined equilibrium, evidence of competition may be difficult to observe (Wiens 1977). Thorman and Wiederholm (1984) concluded that extreme changes in temperature and salinity regulated fish populations in the Bothnian Sea, Sweden, with food competition and resource partitioning being secondary. Tyler (1978) showed that fishes living in areas that have fluctuating physical factors, or are regularly disturbed, have weak prey partitioning. This appears to be true for the Columbia River estuary, which is a highly dynamic system with large seasonal and daily (tidal) fluctuations in temperature, salinity, river flows, fish species abundances, and prey resources. Tyler also speculated that regular physical disruptions may allow the persistence of high densities of r-selected (rapidly reproducing) prey species, which would further weaken food partitioning. Varying salinities (0-32 0/00) and water depths may limit the estuarine distributions of many fish species and disrupt prolonged predation on specific prey in a particular habitat. Therefore, some prey resources may never be reduced to levels that precipitate resource partitioning.

Another reason for the high diet overlaps relates to the number of available prey species. The benthic and epibenthic invertebrates of the Columbia River estuary are dominated by relatively few species which tolerate large changes in salinity (Holton et al. 1984; Williams 1983). Columbia River estuarine fishes may consume similar prey because they are limited to only a few abundant prey species.

If there is potential food competition in the Columbia River estuary, it could be prevented or reduced by the separation of fishes into different habitats (Schoener 1974). There are indications that this occurs in the Columbia River estuary. Separation occurs not only into demersal, pelagic, and intertidal areas, but also into upper, middle, and lower estuarine areas. For example, in the demersal habitat, Pacific staghorn sculpin (a euryhaline species) were found primarily in the middle and lower estuary, whereas prickly sculpin (a freshwater species) were found in the upper estuary. At times, both species feed on _C. salmonis_, but they have effectively separate ranges because of salinity preferences.

The 18 May 1980 eruption of Mount St. Helens and the associated mud and ash deposits affected the feeding habits of some Columbia River estuarine fishes for a short time. Consumption of the primary prey _C. salmonis_ was reduced for American shad and salmonids in June 1980 (Emmett 1982), probably because of the effects of high turbidity, sediment deposition, and ash on _C. salmonis_ (Emmett 1982; Brezezinski and Holton 1983).

Conclusions

We identified essentially three types of feeding among Columbia River estuarine fishes: plankton feeders (e.g., Pacific herring, smelts, and salmonids), benthos feeders (e.g., starry flounder and prickly sculpin), and epibenthos feeders (e.g., Pacific tomcod). Some fish species shifted their diets and guilds as prey types varied in abundance. The diet overlaps for many fishes were high, yet little information exists to indicate competition. Competition and resource partitioning by fishes in the Columbia River estuary may be reduced by widely fluctuating physical parameters (salinity, temperature, river flow, etc.) that promote rapidly reproducing species and prevent prolonged predation on particular prey. The widely changing physical conditions may also allow only a few very abundant prey species to exist, thus reducing resource partitioning. Only a few crustacean species provide the majority of food for the fishes of the Columbia River estuary; the kinds of prey consumed appear to be determined by the seasonal abundances of these species.

In the past century, the Columbia River and its estuary have undergone extreme modification (Neal 1972; Thomas 1983), and future modification is expected. Reductions and alterations of prey habitat (e.g., mudflats) and sources of organic carbon (detritus) which support most of the dominant epibenthic (Simenstad and Cordell 1985) and benthic invertebrates on which fishes feed could deleteriously affect Columbia River estuarine fish production.

Acknowledgments

This study involved the hard work of many individuals. Special thanks go to Keith Verner, Gregory Hammann, Sandy Lipovsky, and John Lock, who analysed some of the stomachs. George McCabe, Jr., Robert McConnell, Travis Coley, and others helped collect the fishes. It was only with the support of these dedicated people that this study was completed. Partial financial support came from the Columbia River Estuary Data Development Program.

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TABLE 1. Columbia River estuarine fish species analyzed for stomach contents February 1980 through January 1981. Primary habitat (P= pelagic, D= demersal, I= intertidal) and sample size are shown for each entry; some species are divided into year classes (2+ indicates 2 years and older).

		Sample size			
Species (age class)	Habitat	Spring	Summer	Fall	Winter
White sturgeon, *Acipenser transmontanus*	D	8	17		
American shad (0), *Alosa sapidissima*	I		40		
American shad (1), *Alosa sapidissima*	D,P	125	91		112
American shad (2+), *Alosa sapidissima*	P	23	15		
Pacific herring (0), *Clupea harengus pallasi*	P	11	119	26	
Pacific herring (1), *Clupea harengus pallasi*	P	56	35		9
Northern anchovy (1), *Engraulis mordax*	P		29		
Chum salmon (0), *Oncorhynchus keta*	I	6			
Coho salmon (juv), *Oncorhynchus kisutch*	P	173			
Sockeye salmon (juv), *Oncorhynchus nerka*	P	22			
Chinook salmon (0), *Oncorhynchus tshawytscha*	I,P	292	423	94	67
Chinook salmon (1), *Oncorhynchus tshawytscha*	P	182			37
Cutthroat trout, *Salmo clarki*	P	8	4		
Steelhead (juv), *Salmo gairdneri*	P	106			
Surf smelt, *Hypomesus pretiosus*	P	58	64	3	25
Longfin smelt (0), *Spirinchus thaleichthys*	P,D		47	34	
Longfin smelt (1), *Spirinchus thaleichthys*	P,D	87	222	37	149
Peamouth, *Mylocheilus caurinus*	I,D		6		4
Threespine stickleback, *Gasterosteus aculeatus*	I				18

TABLE 1. Continued.

Species (age class)	Habitat	Sample size Spring	Summer	Fall	Winter
Shiner perch (0), *Cymatogaster aggregata*	I		33		
Shiner perch (1), *Cymatogaster aggregata*	P		44		
Pacific tomcod, *Microgadus proximus*	D	67	123	48	99
Redtail surfperch, *Amphistichus rhodoterus*	D	4			
Snake prickleback, *Lumpenus sagitta*	D	7			20
Pacific sand lance, *Ammodytes hexapterus*	D	16			
Prickly sculpin, *Cottus asper*	D	84	77	26	56
Pacific staghorn sculpin, *Leptocottus armatus*	D	116	141	48	90
Butter sole, *Isopsetta isolepis*	D	13			
English sole (0), *Parophrys vetulus*	I,D	38	46	20	7
English sole (1), *Parophrys vetulus*	D	19	9		26
Starry flounder (0), *Platichthys stellatus*	I	14	104	29	
Starry flounder (1), *Platichthys stellatus*	D	173	118	48	94
Starry flounder (2+), *Platichthys stellatus*	D	97	39		112
Sand sole, *Psettichthys melanostictus*	D	10			26
TOTAL		1815	1846	413	951

Figure Captions

Fig. 1. Locations of 49 sites sampled monthly in the Columbia River estuary from February 1980 through July 1981.

Fig. 2. Diet overlaps (C) of Columbia River estuarine fishes in spring (April-June) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 3. Food of Columbia River estuarine fishes as measured by Index of Relative Importance (IRI) in spring (April-June) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 4. Diet overlaps (C) of Columbia River estuarine fishes in summer (July-September) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 5. Food of Columbia River estuarine fishes as measured by Index of Relative Importance (IRI) in summer (July-September) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 6. Diet overlaps (C) of Columbia River estuarine fishes in fall (October-December) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 7. Food of Columbia River estuarine fishes as measured by Index of Relative Importance (IRI) in fall (October-December) 1980 in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 8. Diet overlaps (C) of Columbia River estuarine fishes in winter (February-March 1980, January 1981) in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

Fig. 9. Food of Columbia River estuarine fishes as measured by Index of Relative Importance (IRI) in winter (February-March 1980, January 1981) in three habitats (P = pelagic, D = demersal, I = intertidal). Age class is given when known; age class 2+ includes fish 2 years old and older.

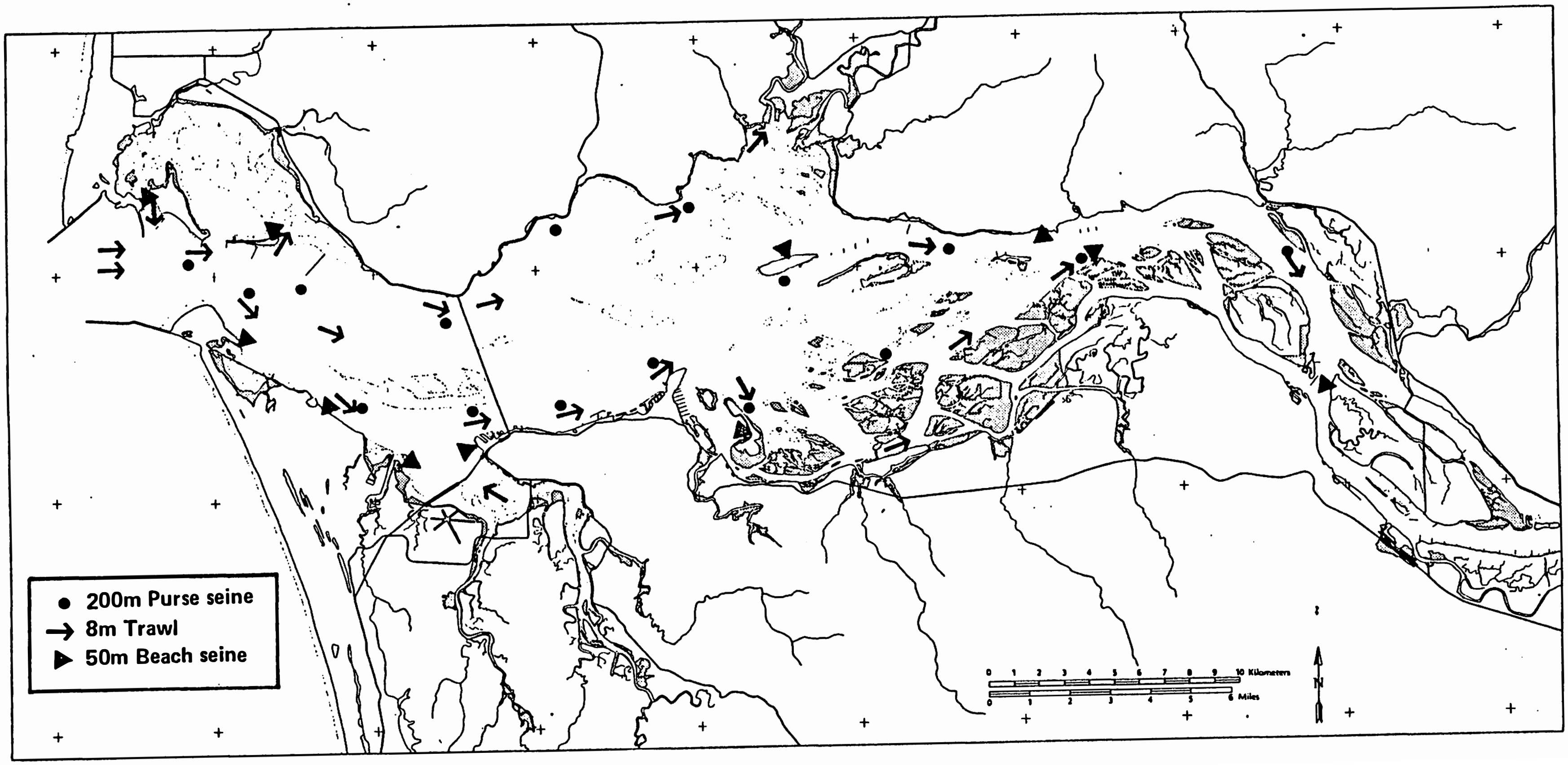

● 200m Purse seine
→ 8m Trawl
▶ 50m Beach seine
0 1 2 3 4 5 6 7 8 9 10 Kilometers
0 1 2 3 4 5 6 Miles
N

Figure 2

SPRING

☐ C < 0.30 ▥ 0.30 ≤ C < 0.60 ▨ C ≥ 0.60

GUILD		HABITAT	English sole (0)	Snake prickleback	Pacific sand lance	Surf Smelt	Pacific herring (1)	Pacific herring (0)	Longfin smelt (1)	American shad (1)	Sockeye salmon	Chum salmon	American shad (2+)	Cutthroat trout	Steelhead	Chinook salmon (0)	Chinook salmon (1)	Coho salmon	White sturgeon	Prickly sculpin	Starry flounder (1)	Starry flounder (2+)	Pacific staghorn sculpin	Starry flounder (0)	English sole (1+)	Butter sole	Redtail surfperch	Pacific tomcod	Sand sole
I	English sole (0)	I, D																											
	Snake prickleback	D	0.84																										
	Pacific sand lance	D	0.80	0.98																									
	Surf smelt	P	0.80	0.98	1.00																								
	Pacific herring (1)	P	0.79	0.97	1.00	1.00																							
	Pacific herring (0)	P	0.86	0.98	0.99	0.99	0.98																						
	Longfin smelt (1)	P, D	0.86	0.97	0.97	0.96	0.96	0.97																					
	American shad (1)	D, P	0.74	0.77	0.74	0.73	0.72	0.76	0.86																				
	Sockeye salmon	P	0.80	0.82	0.79	0.79	0.78	0.81	0.84	0.72																			
	Chum salmon	I	0.64	0.66	0.64	0.64	0.63	0.66	0.67	0.57	0.63																		
	American shad (2+)	P	0.51	0.62	0.49	0.49	0.48	0.51	0.53	0.57	0.49	0.39																	
II	Cutthroat trout	P	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.26	0.01	0.03	0.03																
	Steelhead	P	0.00	0.02	0.00	0.00	0.00	0.00	0.12	0.50	0.02	0.07	0.15	0.75															
	Chinook salmon (0)	I, P	0.00	0.01	0.00	0.00	0.00	0.00	0.14	0.54	0.03	0.23	0.06	0.43	0.82														
	Chinook salmon (1)	P	0.00	0.01	0.00	0.00	0.00	0.00	0.15	0.55	0.03	0.02	0.08	0.48	0.81	0.94													
	Coho salmon	P	0.00	0.01	0.00	0.00	0.00	0.00	0.15	0.55	0.03	0.05	0.06	0.46	0.80	0.95	1.00												
	White sturgeon	D	0.04	0.05	0.04	0.04	0.04	0.04	0.19	0.56	0.06	0.04	0.08	0.41	0.74	0.91	0.97	0.98											
	Prickly sculpin	D	0.00	0.01	0.00	0.00	0.00	0.00	0.15	0.54	0.02	0.01	0.06	0.43	0.76	0.92	0.98	0.99	1.00										
	Starry flounder (1)	D	0.01	0.02	0.01	0.01	0.01	0.01	0.16	0.53	0.03	0.02	0.06	0.40	0.73	0.90	0.97	0.98	1.00	0.99									
	Starry flounder (2+)	D	0.00	0.01	0.00	0.00	0.00	0.00	0.15	0.55	0.02	0.01	0.06	0.43	0.79	0.92	0.96	0.97	0.95	0.96	0.95								
	Pacific staghorn sculpin	D	0.00	0.01	0.00	0.00	0.00	0.00	0.14	0.54	0.02	0.01	0.06	0.42	0.80	0.90	0.92	0.92	0.89	0.90	0.88	0.91							
	Starry flounder (0)	I	0.31	0.26	0.25	0.25	0.25	0.29	0.40	0.75	0.26	0.20	0.21	0.41	0.79	0.88	0.89	0.90	0.88	0.88	0.86	0.89	0.87						
III	English sole (1)	D	0.09	0.03	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
	Butter sole	D	0.09	0.03	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	1.00				
	Redtail surfperch	D	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01			
IV	Pacific tomcod	D	0.10	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.04	0.06	0.01	0.10	0.09	0.05		
	Sand sole	D	0.08	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.06	0.07	0.02	0.00	0.00	0.02	0.93	

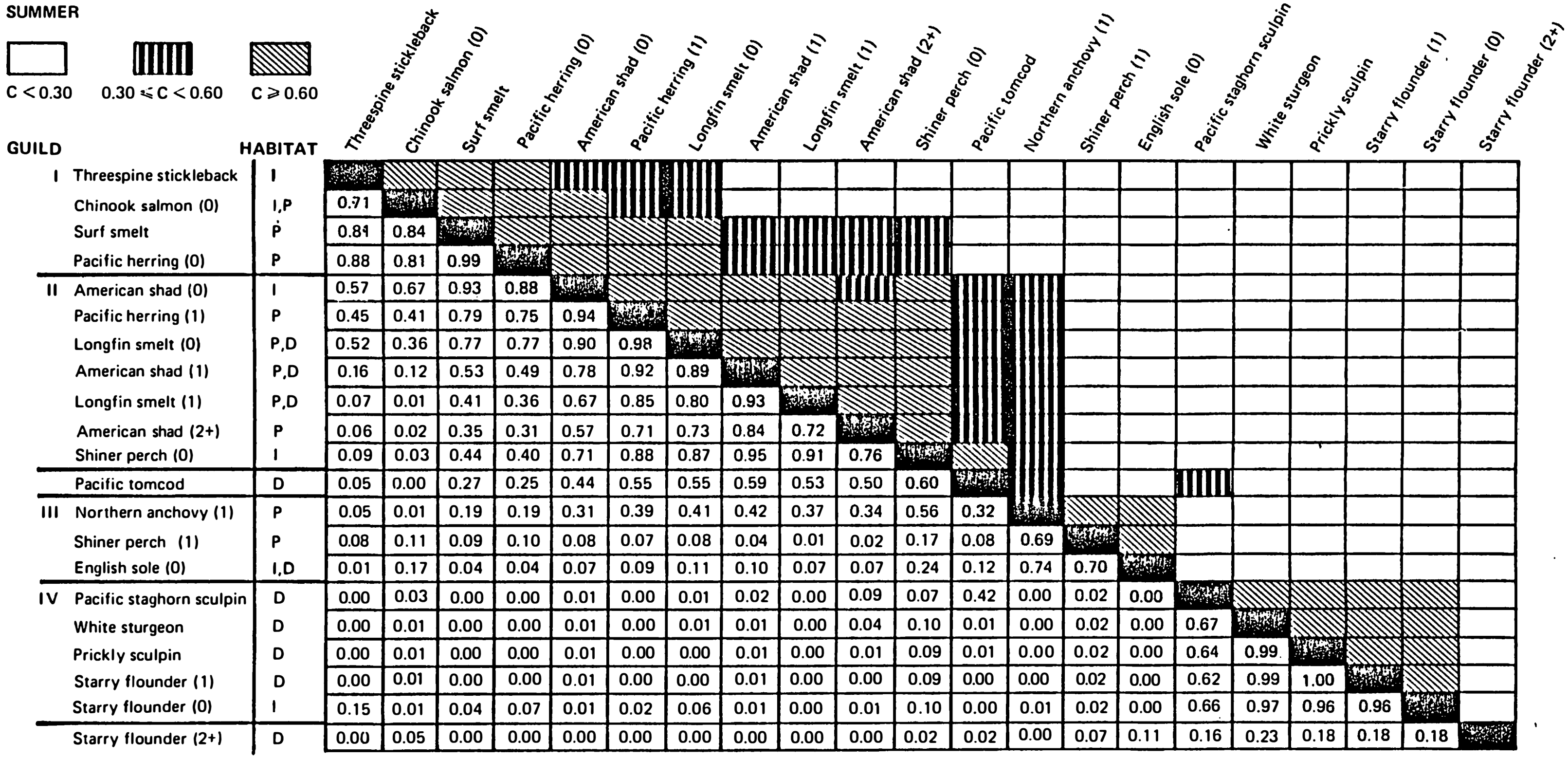
Figure 2

SPRING

▨ Highest IRI ▥ IRI≥ 10%

GUILD		HABITAT	Plant material	Copepoda	Calanoida	Harpacticoida	Cyclopoida	Digested Copepoda	Insect parts	Diptera adult	*Corophium salmonis*	*Corophium spinicorne*	*Archeomysis grebnitzkii*	Cumacea	*Eogammarus spp.*	Dungeness crab megalops	Digested fish	*Thaeichthys pacificus*	*Macoma balthica*
I	English sole (0)	I, D			▨	▥								▥					
	Snake prickleback	D	▥		▨														
	Pacific sand lance	D			▨														
	Surf smelt	P			▨														
	Pacific herring (1)	P			▨														
	Pacific herring (0)	P			▨	▥													
	Longfin smelt (1)	P, D			▨						▥								
	American shad (1)	D, P			▨						▥								
	Sockeye salmon	P			▨		▥	▥											
	Chum salmon	I			▥					▨									
	American shad (2+)	P	▨	▥	▥														
II	Cutthroat trout	P							▨		▥	▥							
	Steelhead	P							▥		▨								
	Chinook salmon (0)	I, P									▨								
	Chinook salmon (1)	P									▨	▥							
	Coho salmon	P									▨								
	White sturgeon	D									▨								
	Prickly sculpin	D									▨								
	Starry flounder (1)	D									▨								
	Starry flounder (2+)	D									▨								▥
	Pacific staghorn sculpin	D									▨						▥		
	Starry flounder (0)	I			▥	▥					▨								
III	English sole (1)	D											▨						
	Butter sole	D											▨						
	Redtail surfperch	D														▨			
IV	Pacific tomcod	D													▨				
	Sand sole	D													▨			▥	

Figure 3

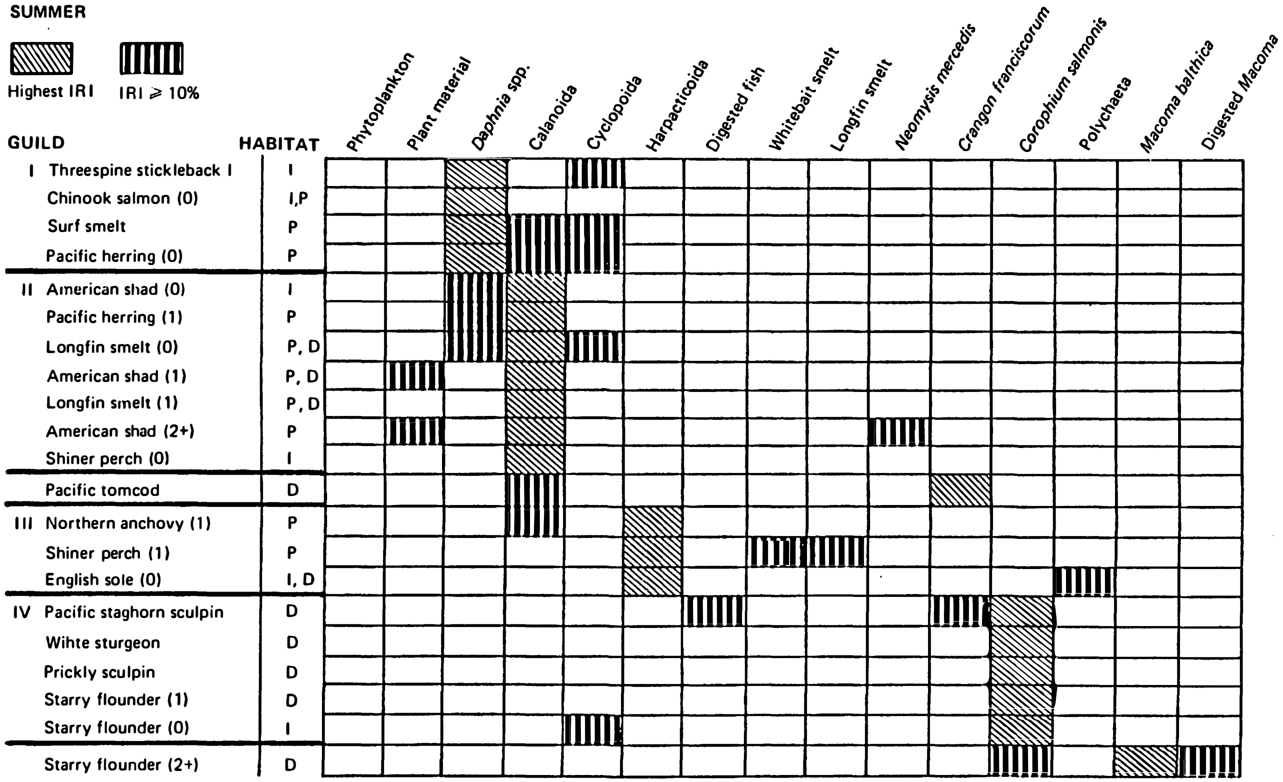


SUMMER

☐ C < 0.30 ▥ 0.30 ≤ C < 0.60 ▨ C ≥ 0.60

GUILD		HABITAT	Threespine stickleback	Chinook salmon (0)	Surf smelt	Pacific herring (0)	American shad (0)	Pacific herring (1)	Longfin smelt (0)	American shad (1)	Longfin smelt (1)	American shad (2+)	Shiner perch (0)	Pacific tomcod	Northern anchovy (1)	Shiner perch (1)	English sole (0)	Pacific staghorn sculpin	White sturgeon	Prickly sculpin	Starry flounder (1)	Starry flounder (0)	Starry flounder (2+)
I	Threespine stickleback	I	■	▨	▨	▨	▥	▥	▥														
	Chinook salmon (0)	I,P	0.71	■	▨	▨	▨	▥	▥														
	Surf smelt	P	0.81	0.84	■	▨	▨	▨	▨	▥	▥	▥	▥										
	Pacific herring (0)	P	0.88	0.81	0.99	■	▨	▨	▨	▥	▥	▥	▥										
II	American shad (0)	I	0.57	0.67	0.93	0.88	■	▨	▨	▨	▨	▥	▨	▥	▥								
	Pacific herring (1)	P	0.45	0.41	0.79	0.75	0.94	■	▨	▨	▨	▨	▨	▥	▥								
	Longfin smelt (0)	P,D	0.52	0.36	0.77	0.77	0.90	0.98	■	▨	▨	▨	▨	▥	▥								
	American shad (1)	P,D	0.16	0.12	0.53	0.49	0.78	0.92	0.89	■	▨	▨	▨	▥	▥								
	Longfin smelt (1)	P,D	0.07	0.01	0.41	0.36	0.67	0.85	0.80	0.93	■	▨	▨	▥	▥								
	American shad (2+)	P	0.06	0.02	0.35	0.31	0.57	0.71	0.73	0.84	0.72	■	▨	▥	▥								
	Shiner perch (0)	I	0.09	0.03	0.44	0.40	0.71	0.88	0.87	0.95	0.91	0.76	■	▨	▥								
	Pacific tomcod	D	0.05	0.00	0.27	0.25	0.44	0.55	0.55	0.59	0.53	0.50	0.60	■	▥			▥					
III	Northern anchovy (1)	P	0.05	0.01	0.19	0.19	0.31	0.39	0.41	0.42	0.37	0.34	0.56	0.32	■	▨	▨						
	Shiner perch (1)	P	0.08	0.11	0.09	0.10	0.08	0.07	0.08	0.04	0.01	0.02	0.17	0.08	0.69	■	▨						
	English sole (0)	I,D	0.01	0.17	0.04	0.04	0.07	0.09	0.11	0.10	0.07	0.07	0.24	0.12	0.74	0.70	■						
IV	Pacific staghorn sculpin	D	0.00	0.03	0.00	0.00	0.01	0.00	0.01	0.02	0.00	0.09	0.07	0.42	0.00	0.02	0.00	■	▨	▨	▨	▨	
	White sturgeon	D	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.01	0.00	0.04	0.10	0.01	0.00	0.02	0.00	0.67	■	▨	▨	▨	
	Prickly sculpin	D	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.09	0.01	0.00	0.02	0.00	0.64	0.99	■	▨	▨	
	Starry flounder (1)	D	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.09	0.00	0.00	0.02	0.00	0.62	0.99	1.00	■	▨	
	Starry flounder (0)	I	0.15	0.01	0.04	0.07	0.01	0.02	0.06	0.01	0.00	0.01	0.10	0.00	0.01	0.02	0.00	0.66	0.97	0.96	0.96	■	
	Starry flounder (2+)	D	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.07	0.11	0.16	0.23	0.18	0.18	0.18	■

Figure 4

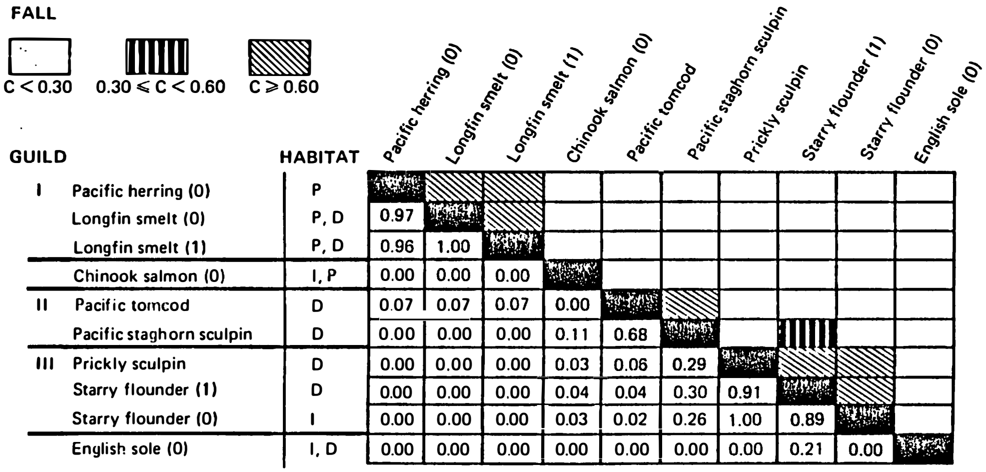


SUMMER

▨ Highest IRI ▥ IRI ≥ 10%

GUILD		HABITAT	Phytoplankton	Plant material	*Daphnia spp.*	Calanoida	Cyclopoida	Harpacticoida	Digested fish	Whitebait smelt	Longfin smelt	*Neomysis mercedis*	*Crangon franciscorum*	*Corophium salmonis*	Polychaeta	*Macoma balthica*	Digested *Macoma*
I	Threespine stickleback I	I			▨		▥										
	Chinook salmon (0)	I,P			▨												
	Surf smelt	P			▨	▥	▥										
	Pacific herring (0)	P			▨	▥	▥										
II	American shad (0)	I			▥	▨											
	Pacific herring (1)	P			▥	▨											
	Longfin smelt (0)	P, D			▥	▨	▥										
	American shad (1)	P, D		▥		▨											
	Longfin smelt (1)	P, D				▨											
	American shad (2+)	P		▥		▨						▥					
	Shiner perch (0)	I				▨											
	Pacific tomcod	D				▥							▨				
III	Northern anchovy (1)	P				▥		▨									
	Shiner perch (1)	P						▨		▥	▥						
	English sole (0)	I, D						▨							▥		
IV	Pacific staghorn sculpin	D							▥				▥	▨			
	Wihte sturgeon	D												▨			
	Prickly sculpin	D												▨			
	Starry flounder (1)	D												▨			
	Starry flounder (0)	I					▥							▨			
	Starry flounder (2+)	D												▥		▨	▥

Figure 5



FALL

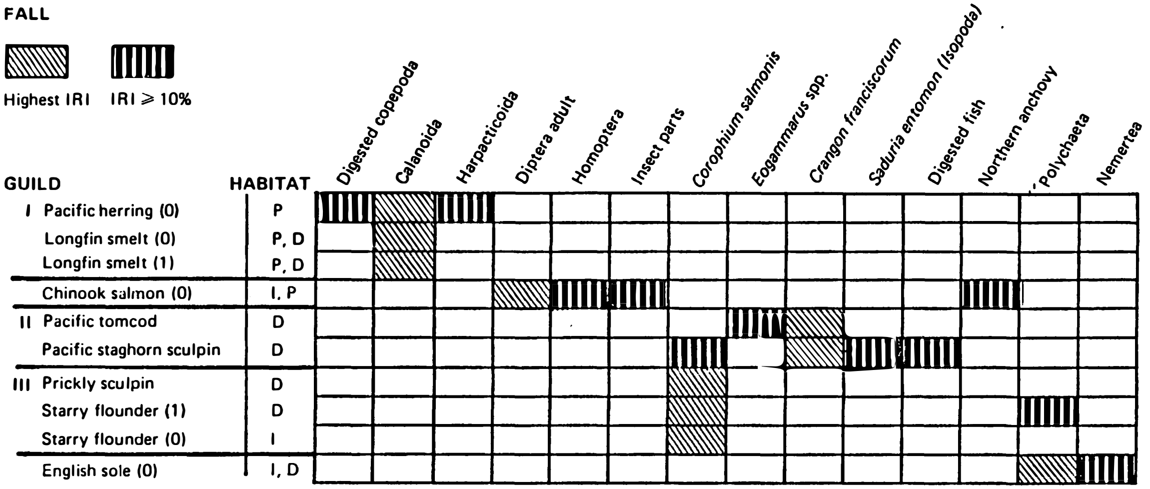
☐ C < 0.30

▥ 0.30 ≤ C < 0.60

▨ C ≥ 0.60

GUILD		HABITAT	Pacific herring (0)	Longfin smelt (0)	Longfin smelt (1)	Chinook salmon (0)	Pacific tomcod	Pacific staghorn sculpin	Prickly sculpin	Starry flounder (1)	Starry flounder (0)	English sole (0)
I	Pacific herring (0)	P	■	▨	▨							
	Longfin smelt (0)	P, D	0.97	■	▨							
	Longfin smelt (1)	P, D	0.96	1.00	■							
	Chinook salmon (0)	I, P	0.00	0.00	0.00	■						
II	Pacific tomcod	D	0.07	0.07	0.07	0.00	■	▨				
	Pacific staghorn sculpin	D	0.00	0.00	0.00	0.11	0.68	■		▥		
III	Prickly sculpin	D	0.00	0.00	0.00	0.03	0.06	0.29	■	▨	▨	
	Starry flounder (1)	D	0.00	0.00	0.00	0.04	0.04	0.30	0.91	■	▨	
	Starry flounder (0)	I	0.00	0.00	0.00	0.03	0.02	0.26	1.00	0.89	■	
	English sole (0)	I, D	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	■

Figure 6

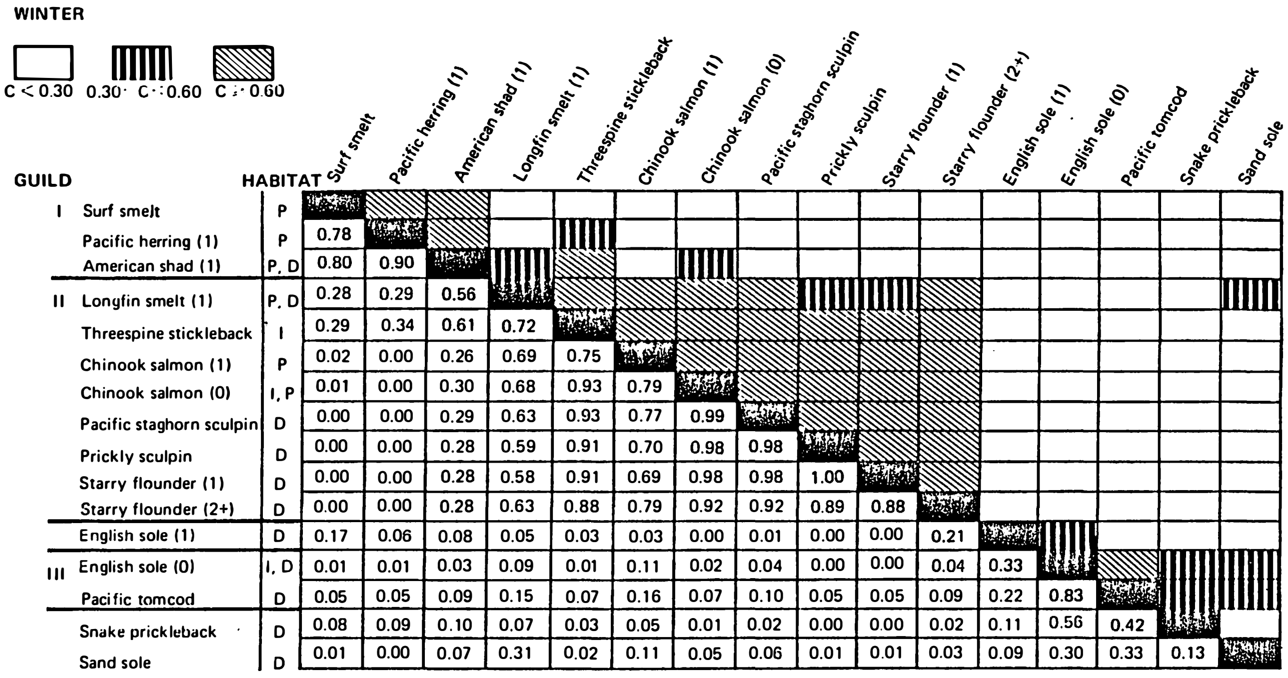


FALL

▨ Highest IRI ▥ IRI ≥ 10%

GUILD		HABITAT	Digested copepoda	Calanoida	Harpacticoida	Diptera adult	Homoptera	Insect parts	*Corophium salmonis*	*Eogammarus* spp.	*Crangon franciscorum*	*Saduria entomon* (Isopoda)	Digested fish	Northern anchovy	Polychaeta	Nemertea
I	Pacific herring (0)	P	▥	▨	▥											
	Longfin smelt (0)	P, D		▨												
	Longfin smelt (1)	P, D		▨												
	Chinook salmon (0)	I, P				▨	▥	▥						▥		
II	Pacific tomcod	D								▥	▨					
	Pacific staghorn sculpin	D							▥		▨	▥	▥			
III	Prickly sculpin	D							▨							
	Starry flounder (1)	D							▨						▥	
	Starry flounder (0)	I							▨							
	English sole (0)	I, D													▨	▥

Figure 7

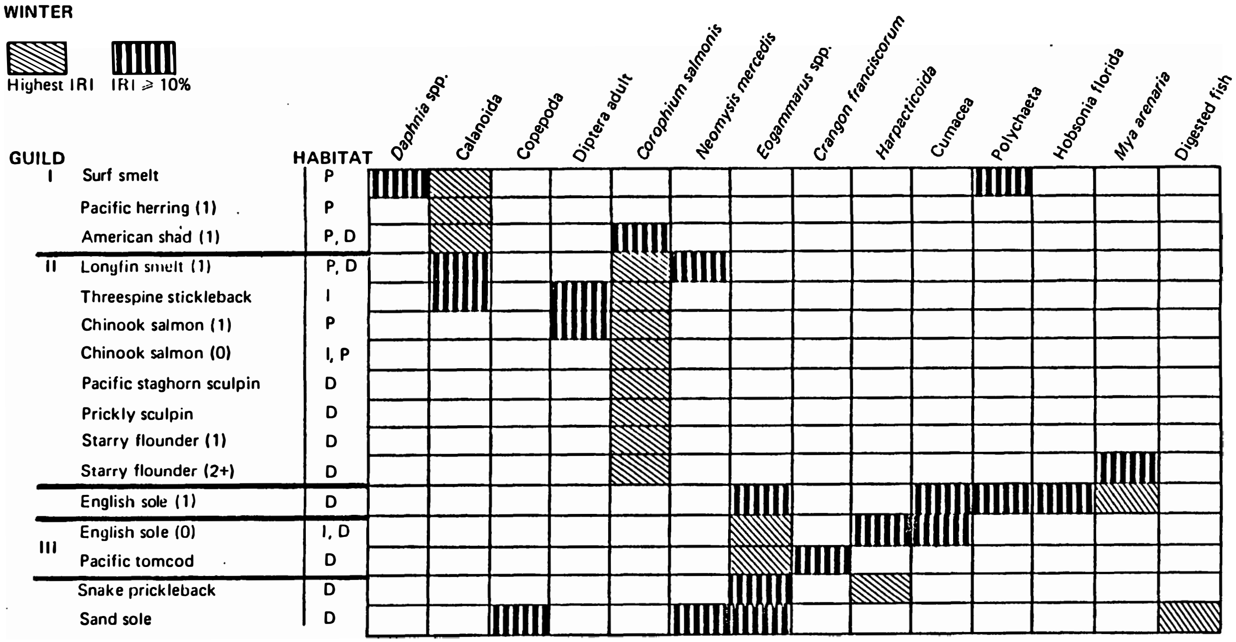


WINTER

□ C < 0.30   ▥ 0.30 ≤ C ≤ 0.60   ▨ C > 0.60

GUILD		HABITAT	Surf smelt	Pacific herring (1)	American shad (1)	Longfin smelt (1)	Threespine stickleback	Chinook salmon (1)	Chinook salmon (0)	Pacific staghorn sculpin	Prickly sculpin	Starry flounder (1)	Starry flounder (2+)	English sole (1)	English sole (0)	Pacific tomcod	Snake prickleback	Sand sole
I	Surf smelt	P	■	▨	▨													
	Pacific herring (1)	P	0.78	■	▨		▥											
	American shad (1)	P, D	0.80	0.90	■	▥	▨		▥									
II	Longfin smelt (1)	P, D	0.28	0.29	0.56	■	▨	▨	▨	▨	▥	▥	▨					▥
	Threespine stickleback	I	0.29	0.34	0.61	0.72	■	▨	▨	▨	▨	▨	▨					
	Chinook salmon (1)	P	0.02	0.00	0.26	0.69	0.75	■	▨	▨	▨	▨	▨					
	Chinook salmon (0)	I, P	0.01	0.00	0.30	0.68	0.93	0.79	■	▨	▨	▨	▨					
	Pacific staghorn sculpin	D	0.00	0.00	0.29	0.63	0.93	0.77	0.99	■	▨	▨	▨					
	Prickly sculpin	D	0.00	0.00	0.28	0.59	0.91	0.70	0.98	0.98	■	▨	▨					
	Starry flounder (1)	D	0.00	0.00	0.28	0.58	0.91	0.69	0.98	0.98	1.00	■	▨					
	Starry flounder (2+)	D	0.00	0.00	0.28	0.63	0.88	0.79	0.92	0.92	0.89	0.88	■					
	English sole (1)	D	0.17	0.06	0.08	0.05	0.03	0.03	0.00	0.01	0.00	0.00	0.21	■	▥			
III	English sole (0)	I, D	0.01	0.01	0.03	0.09	0.01	0.11	0.02	0.04	0.00	0.00	0.04	0.33	■	▨	▥	▥
	Pacific tomcod	D	0.05	0.05	0.09	0.15	0.07	0.16	0.07	0.10	0.05	0.05	0.09	0.22	0.83	■	▥	▥
	Snake prickleback	D	0.08	0.09	0.10	0.07	0.03	0.05	0.01	0.02	0.00	0.00	0.02	0.11	0.56	0.42	■	
	Sand sole	D	0.01	0.00	0.07	0.31	0.02	0.11	0.05	0.06	0.01	0.01	0.03	0.09	0.30	0.33	0.13	■

Figure 8.



WINTER

▨ Highest IRI ▥ IRI ≥ 10%

GUILD		HABITAT	*Daphnia* spp.	Calanoida	Copepoda	Diptera adult	*Corophium salmonis*	*Neomysis mercedis*	*Eogammarus* spp.	*Crangon franciscorum*	Harpacticoida	Cumacea	Polychaeta	*Hobsonia florida*	*Mya arenaria*	Digested fish
I	Surf smelt	P	▥	▨									▥			
	Pacific herring (1)	P		▨												
	American shad (1)	P, D		▨			▥									
II	Longfin smelt (1)	P, D		▥			▨	▥								
	Threespine stickleback	I		▥		▥	▨									
	Chinook salmon (1)	P				▥	▨									
	Chinook salmon (0)	I, P					▨									
	Pacific staghorn sculpin	D					▨									
	Prickly sculpin	D					▨									
	Starry flounder (1)	D					▨									
	Starry flounder (2+)	D					▨								▥	
	English sole (1)	D							▥			▥	▥	▥	▨	
III	English sole (0)	I, D							▨		▥	▥				
	Pacific tomcod	D							▨	▥						
	Snake prickleback	D							▥		▨					
	Sand sole	D			▥			▥	▥							▨

Figure 9