FOOD HABITS OF JUVENILE SALMON IN THE OREGON COASTAL ZONE, JUNE 1979

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ABSTRACT

Euphausiids, hyperiid amphipods, crab larvae, and fishes were the important prey identified from stomachs of 408 juvenile salmon collected in a purse seine along the Oregon coast in June 1979. Food habits of juvenile salmon differed among species. About 95% of the weight and numbers of prey of chum salmon consisted of euphausiids and hyperiids. Euphausiids and hyperiids were numerically the most abundant prey items of juvenile coho and chinook salmon, but, on a weight basis, over half the stomach contents consisted of fishes.

Variability in food habits was high for both juvenile coho and chinook salmon. Fishes from only 2 of 45 station pairs (coho) and 3 of 28 (chinook) had diet similarities >75%. The statistical relationship between weight of euphausiids and weight of fishes in stomachs for coho and chinook juveniles showed a strong tendency for both species to contain large amounts of either fishes or euphausiids, but not both simultaneously.

Diet overlap between coho and chinook juveniles was high overall, but low between the same 20 mm size classes of these same species. Euphausiids were eaten in equal numbers throughout the 100-200 mm coho size range; euphausiids were not eaten by chinook <180 mm fork length. Hyperiids were mainly eaten by 180-220 mm coho and by 140-180 mm chinook. Fishes were consumed mainly by juveniles of both species >160 mm.

Based on estimated zooplankton standing stocks, an average (160 mm) coho salmon would have to search and consume all prey in a minimum volume of about 2-8 m^3 per day to fill its stomach. The average abundance of juvenile coho, as determined from purse seining, was 1 smolt per 11,500 m^3, or about 1,440-5,760 times the minimum search volume. These data are related to the question of whether food limitation exists for juvenile salmonids in the sea.

Our knowledge of the ecology of salmon in the ocean, especially during early juvenile life, is scant compared with our understanding of the freshwater phase of salmon life. The first few months that juvenile salmon spend at sea have been identified as a critical period when year-class success may be affected (Gunsolus 1978[3]; Walters et al. 1978; Healey 1980). Basic studies of abundance and distribution, growth, mortality, and feeding habits of young salmon during their first few months at sea are needed to evaluate how the ocean environment and the density of juvenile salmon affect the production of adult salmon.

This paper contributes new information on feeding habits of juveniles of three species of salmon off the Oregon coast: coho, *Oncorhynchus kisutch*; chinook, *O. tshawytscha*; and chum, *O. keta*, salmon. The authors describe the food habits of each species, variability in food habits among fishes collected at different stations, diet overlap between coho and chinook, and speculate on the impact of foraging juvenile coho on zooplankton populations in coastal waters.

METHODS

Fish were collected in a purse seine 457 m long × 30 m deep, constructed of 32 mm stretch mesh with 30 meshes of 127 mm mesh along the bottom of the net. The maximum volume of water encompassed by a round haul set that fished to 10 m depth was calculated to be no more than $1.5 \times 10^5 m^3$. A total of 56 purse seine sets were made between 18 and 29 June 1979 in three regions of the Oregon coastal zone: Off the Columbia River (northern Oregon), off Newport (central Oregon), and in the vicinity of Coos Bay (southern Oregon) (Fig. 1). A total of 509 salmonids <35 cm FL (fork length) (henceforth called juveniles)

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[3]Gunsolus, R. T. 1978. The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Intern. rep., 59 p. Oregon Department of Fish and Wildlife, Clackamas Laboratory, 17330 S.E. Evelyn Street, Clackamas, OR 97015.

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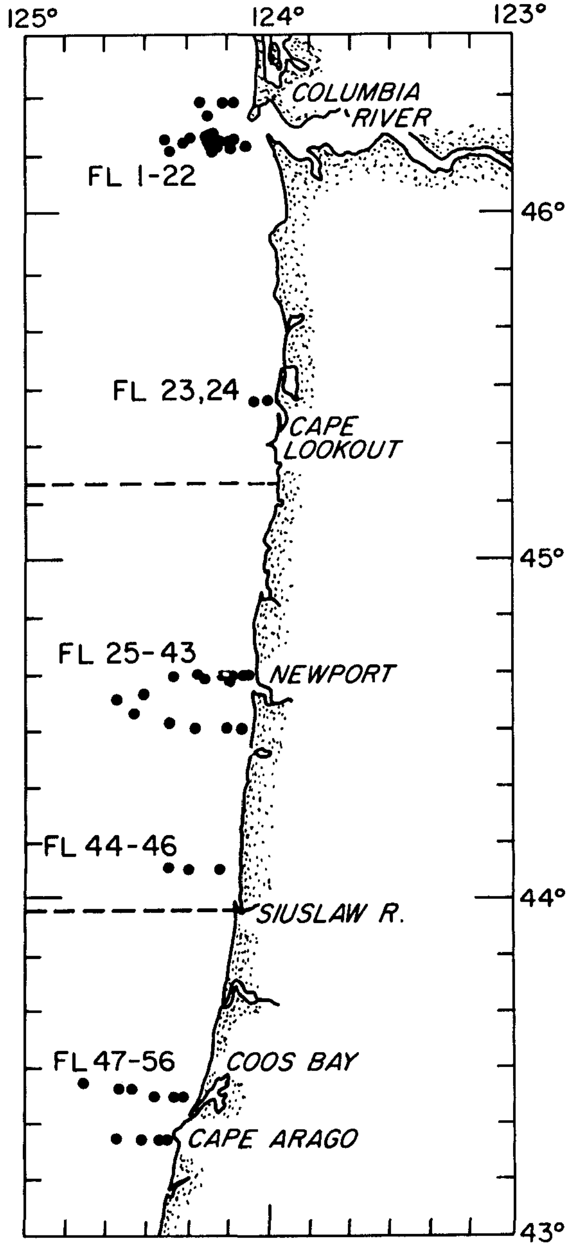

FIGURE 1.—Location of the 56 purse seine sets made by the FV *Flamingo* (FL), 18-29 June 1979. Three geographical regions were arbitrarily defined as northern (FL 1-24), central (FL 25-46), and southern (FL 47-56).

were collected in the sets. Stomach contents of 220 juvenile coho, 147 juvenile chinook, and 41 juvenile chum salmon were examined.

Whole fish <35 cm FL were preserved at sea, after slitting the body cavity, in a 5-15% Formalin[4]-seawater mixture. In the laboratory, all juvenile salmonids were identified to species, measured (fork length), and stomachs removed. Relative stomach fullness was visually estimated on a scale of 0-3 (where 0 = empty; 1, 2, and 3 = fullness in thirds; distended stomachs = 3). State of digestion was noted as one of three subjective categories: Well-digested, partially digested, or fresh. Due to the possibility of differential digestion times of prey items, categorization of state of digestion probably has little meaning except for the "fresh" category.

Food items were identified to the lowest possible taxonomic level and enumerated. Crustaceans and fishes were also identified to developmental stage. Standard length of all fish prey was measured as well as total length of most of the invertebrate taxa from the coho salmon stomachs. Euphausiid lengths were measured from the posterior edge of the eye socket to the tip of the telson. Stomach contents of all salmonids were sorted into major taxonomic groups, damp-dried on absorbent paper, and weighed to the nearest 0.01 g.

RESULTS

Occurrence and Abundances of Prey Taxa

Table 1 lists the average abundances of major taxa of prey in salmonid stomachs and the average length and length ranges of fishes examined. Euphausiids, amphipods, and crab larvae were the most numerous taxa in the stomachs of juveniles of all three species. Fishes were the only other major taxa found in all juvenile salmon. Numbers of fish per stomach were low. On a weight basis, fishes were the most important prey for juvenile coho and chinook, followed by euphausiids (Table 2). Chum stomachs contained mostly euphausiids and amphipods.

Based on percent frequency of occurrence of prey in stomachs, euphausiids occurred in 85% of all chum stomachs, 63% of coho stomachs, and about 50% of chinook and steelhead stomachs (Table 2). Amphipods also ranged in frequency of occurrence from 56 to 32% among these same species. The occurrence of fishes, on the other hand, ranged from 10% of the chum stomachs to 69 and 71% in coho and chinook stomachs, respectively.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Average number of prey in individual stomachs of juvenile chum, coho, and chinook salmon. A more detailed taxonomic breakdown is given in Table 3.

Prey category	Chum	Coho	Chinook
Euphausiids	44.4	36.9	71.9
Amphipods	30.8	28.0	22.9
Fishes	1.2	4.0	4.2
Crab larvae	2.0	13.5	9.9
Copepods	1.6	6.5	3.2
Molluscs	—	10.6	1.7
Barnacle cyprids	—	4.5	—
Shrimp larvae	—	3.0	1.3
Number of stomachs	41	220	146
Number of empty stomachs	5	22	14
Average length of salmonid (mm)	124	164	208
Range in length (mm)	102-144	94-134	89-308

TABLE 2.—Average wet weight (in grams) of major prey groups found in juvenile chum, coho, and chinook salmon stomachs. Numbers in parentheses are percentages of salmon stomachs containing the specific prey item. Average weight of stomach contents is for fish with food in their stomachs. Weights of salmon are wet weights calculated from mean lengths using the length-weight equations of Healey (1980).

	Chum		Coho		Chinook	
Prey category	Wt.	%	Wt.	%	Wt.	%
Euphausiids	0.22	(85)	0.35	(63)	0.63	(51)
Amphipods	0.04	(56)	0.20	(43)	0.12	(31)
Fishes	0.07	(10)	0.73	(69)	1.04	(71)
All others	0.04	(7)	0.12	(88)	0.46	(70)
Average weight of stomach contents (g)	0.28		0.93		1.30	
Average weight of salmon (g)	23.5		55.3		140.7	
Stomach contents as % body weight	1.2		1.7		0.9	

Total weight of stomach contents of each of the three species of juvenile salmon reflects the size of the fishes sampled (Table 2). Weights of stomach contents expressed as percent of total body weight are similar, however, averaging about 1.3%.

Frequencies of occurrence and average abundances of specific prey taxa for each of the three juvenile salmon are shown in Table 3 and are referred to in the following discussion of the diets for each of the species.

Chum Salmon

The diet of chum salmon consisted mainly of the euphausiid *Thysanoëssa spinifera* and the hyperiid amphipod *Hyperoche medusarum*. Mean numerical abundances of *T. spinifera* per chum stomach collected from northern, central, and southern Oregon were 30.1, 149.7, and 3.7, respectively; abundances of hyperiids were 2.9, 104.8, and 17.5, respectively. Both these prey were most common in chum salmon stomachs collected off central Oregon, but sample sizes were so small that it is difficult to attach any real significance to these differences.

Coho Salmon

A total of 19 invertebrate and 13 fish taxa were identified from coho stomachs (Table 3). Major prey items were juvenile euphausiids (*T. spinifera*, average length about 9.0 mm), unidentified hyperiid amphipods (average length about 4.5 mm), and various fishes (most between 25 and 30 mm long). The most frequently occurring fish identified from the juvenile coho stomachs were Pacific sand lance, *Ammodytes hexapterus*; juvenile rockfishes, *Sebastes* spp.; and larval or juvenile stages of several species of flatfishes, clupeids, and osmerids.

Average length of the prey euphausiid, *T. spinifera*, was directly related to length of the juvenile coho predator. The slope of the regression line (Fig. 2) was significantly different from zero ($r = 0.46$, 28 df, $P \sim 0.01$), indicating that coho between 100 and 210 mm long eat progressively larger euphausiids. Juvenile coho fed on a broad spectrum of fish prey sizes, but, again, larger fish often consumed larger prey. Coho 141-180 mm long fed mainly on fish that were 11-30 mm long, whereas 181-200 mm coho consumed mostly larger fishes, ranging from 21 to 40 mm long (Table 4). However, the regression of lengths of whole prey fishes on lengths of juvenile coho, 94-220 mm, was not significantly different from zero.

Relationships between size of coho and numbers and sizes of prey were studied for 87 juve-

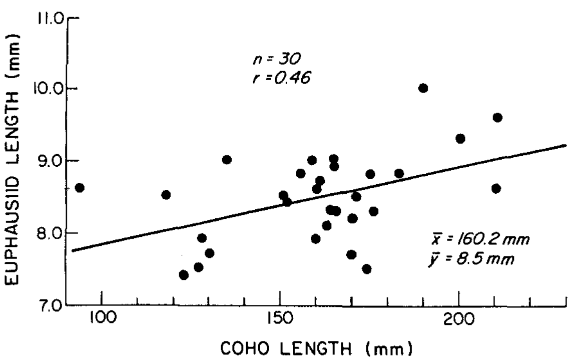

FIGURE 2.—The relationship between coho length and mean euphausiid prey length.

TABLE 3.—Frequency of occurrence (f/n %) and average abundance ($\bar{x}$) of prey found in stomachs of juvenile chum, coho, and chinook salmon.

Prey taxa	Chum		Coho		Chinook	
	f/n %	$\bar{x}$	f/n %	$\bar{x}$	f/n %	$\bar{x}$
Euphausiids						
Thysanoëssa spinifera (9 mm)	83	44.1	56	2.0	53	80.9
T. spinifera (22 mm)	2	2.0	15	2.2	5	1.9
Euphausia pacifica (18 mm)	2	1.0	8	2.0	3	14.5
Unidentified	10	12.7			5	4.3
Amphipods						
Parathemisto pacifica	15	1.2			8	1.6
Hyperoche medusarum	34	46.7			20	42.2
Primno macropa					2	1.0
Unidentified Hyperiidae	15	7.8	44	30.1	19	35.7
Gammaridae (*Atylus tridens*)			11	5.0	12	2.1
Fishes						
Ammodytidae						
Ammodytes hexapterus	10	1.2	30	2.4	32	2.0
Pleuronectiformes						
Isopsetta isolepis			1	1.0		
Citharichthys spp.			1	1.3		
Psettichthys melanostictus			1	1.0		
Unidentified flatfish			8	1.8	32	7.8
Hexagrammidae			3	1.6		
Gadidae			1	1.3	2	1.3
Cottidae					11	1.8
Hemilepidotus spp.			3	4.8		
Unidentified			3	1.6		
Clupeidae			6	3.1	3	2.2
Osmeridae			5	3.2	3	3.0
Scorpaenidae						
Sebastes spp.			15	3.5	8	1.4
Unidentified and Digested	10	2.5	45	3.1	48	1.7
Crab Larvae						
Cancer magister megalopae			16	4.2	9	1.8
Cancer spp. megalopae			16	0.6		
Pinnotheridae zoeae			10	4.7	3	19.2
Pinnotheridae megalopae					12	16.2
Paguridae zoeae					3	2.0
Copepods						
Calanus cristatus			6	8.1	1	12.0
C. marshallae			4	2.0		
Eucalanus bungii			4	1.0		
Epilabidocera longipedata			1	1.0		
Unidentified	12	1.6			3	1.0
Molluscs						
Limacina helicina			7	10.6	2	1.7
Cephalopods					1	1.0
Miscellaneous Arthropods						
Juvenile Crabs					4	14.0
Decapod shrimp mysis	2	2.0	6	2.5	6	1.0
Pandalus jordani zoeae			4	1.0	3	1.3
Barnacle cyprids	2	1.0	7	4.4		
Mysids			3	1.2	2	1.3
Insects	2	1.0	2	1.2	1	1.0
Chaetognatha						
Sagitta elegans	2	5.0	1	1.0		
Polychaetes						
Tomopteris sp.			1	6.5		

TABLE 4.—Frequency distribution of lengths of fish prey found in stomachs of juvenile coho salmon of various lengths.

Standard length of coho (mm)	Number of coho	Length of fish prey (mm)						
		0-10	11-20	21-30	31-40	41-50	51-60	>60
81-100	1		1	1				
101-120	3		3	1				
121-140	36	3	7	10	1	4		
141-160	66		27	35	4	4	1	1
161-180	70	8	69	80	28	21	2	
181-200	30		5	25	23	3	4	
201-220	7			7		1	1	

nile coho with stomachs full of fresh material to minimize the problem of differential digestion rates of various prey items. No statistically significant differences ($P>0.05$) were found between length of coho and either number of euphausiids, total number of prey items, or numbers of fishes. Significantly greater numbers of hyperiid amphipods occurred, however, in larger than in smaller coho (Fig. 3). Average weight of fishes in stomachs also increased with length of juvenile coho. Total weight of stomach contents was related to length of juvenile coho (weight of prey = −1.0 + 0.016 × length of coho, $r = 0.43$, $P<0.01$). The relationship between the two food groups most important to juvenile coho was investigated by plotting weights of euphausiids versus weights of fishes in the stomachs for each of the 87 coho. This plot was divided into quadrants by drawing lines parallel to the abscissa and ordinate at the median values of euphausiid and fish weight. The numbers of data points in each quadrant are shown in a 2 × 2 contingency table (Table 5). The χ^2 of 12.5 was highly significant ($P<0.01$, 1 df), indicating a strong tendency for juvenile coho to contain large amounts by weight of either fishes or euphausiids, but not both at the same time. Of these 87 coho, 26% contained only fishes and 21% only euphausiids. This trend may be a result of active selection of one type of prey or a result of prey patchiness. The latter explanation may be more plausible, since stratification of these two prey groups in the stomachs was evident in those individuals containing both prey items.

TABLE 5.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 87 juvenile coho salmon.

		Euphausiid prey (g)	
		<0.24	>0.24
Fish prey (g)	>0.48	31	13
	<0.48	13	30

Variability in the composition of stomach contents of coho salmon was often high among the 10 stations where at least six fish were analyzed per station (Table 6). For example, juvenile euphausiids were the most numerically abundant prey taxa at four stations (2, 3, 12, and 29); hyperiid amphipods at four other stations (10, 27, 28, and 39); and fishes and crab larvae at one station each. The differences in feeding habits among stations were compared by calculating similarity indices for all possible station pairs. We used the percent similarity index (PSI = $\Sigma \min P_i$), where

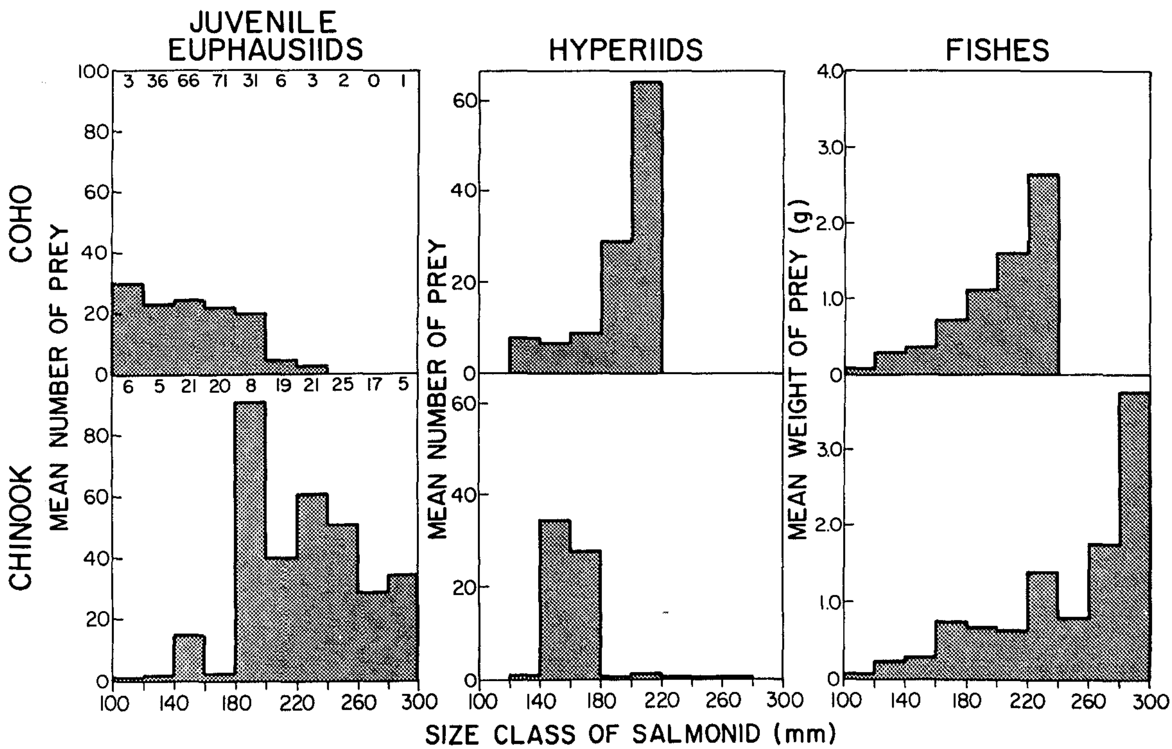

FIGURE 3.—Average abundance of juvenile euphausiids and hyperiids and average weight of fish prey occurring in the stomachs of each 20 mm size class of juvenile coho and chinook salmon. The averages are taken over only those stomachs in which prey items occurred. The numbers at the top of the leftmost figure denote the sample size in each 20 mm size class.

TABLE 6.—Sampling data and percent of total numbers of major prey items found in juvenile coho stomachs off the Oregon coast (only at those stations where six or more juvenile coho were taken). Includes only those prey taxa comprising 2% or more of the total number of prey items.

	Northern Oregon						Central Oregon			
Station	1	2	3	10	12	22	27	28	29	39
Time of day	0630	0900	1000	1730	0800	1500	0930	1130	1300	0900
Day in June	18	18	18	19	20	21	23	23	23	27
Water depth (m)	40	77	102	66	77	130	55	77	73	55
Distance from shore (km)	11.8	19.4	25.9	13.3	19.1	33.3	10.0	16.3	27.0	9.4
Number of coho examined	33	14	16	32	37	30	8	6	11	8
Average length of coho (mm)	158	175	158	154	158	163	165	161	157	193
Percent of coho with empty or nearly empty stomachs	58	79	69	25	8	20	12	33	0	0
Thysanoëssa spinifera (juveniles)	8.9	68.3	41.4	6.3	93.4	12.1	9.8	2.6	53.5	3.4
Hyperiid amphipods	20.1	22.5	26.9	36.0		13.0	39.7	89.9	30.7	94.0
Fishes	42.0	2.9	8.4	10.7	6.0	8.4	29.3			
Crab megalops				16.5		26.1				
Crab zoea			4.0			24.0				
Pteropods									9.2	
Calanus cristatus							6.5		4.9	
Cancer magister megalops			4.9	17.0		4.9				
Gammarid amphipods			6.2			7.7				
T. spinifera (adult)	16.6	2.1								
Barnacle cyprids			3.1	9.3		2.2				
Euphausia pacifica	9.5		3.1							
Total number of prey items	169	378	227	364	2,516	1,135	174	306	1,745	1,326

P_i is the proportion of the ith taxa (based on numbers of individual prey) in a stomach (Whittaker 1960), and PSI between a pair of stations is calculated by summing the smaller (minimum) P_i's for all food items. Similarity was generally low (<50%) among stations. Only 6 of the 45 possible pairings showed similarities >66% (stations 2-3, 2-12, 2-29, 3-29, 10-27, and 28-39), and only two pairs had a similarity >75% (2-29 and 28-39).

Some of this variability among stations may be related to the geographical regions sampled. For example, the numerical percentage of euphausiids averaged 45.5% for coho caught near the Columbia River plume (stations 1-22) compared with 17.4% off the central Oregon coast (stations 27-39, Table 6). Fishes occurred in the diets at all stations and made up 14% of the total prey numbers in the Columbia River area, whereas they were a significant part of coho diets at only one of four stations off Newport. Amphipods occurred more frequently in the stomach contents off Newport, averaging 63.6% of the total number, compared with 20.1% in coho from the Columbia River plume. The copepod, *Calanus cristatus*, and pteropod, *Limacina helicina*, were important components of the diets of only those juvenile coho caught off the central Oregon coast. An additional component of among-station variability may be attributed to differences in diet between inshore and offshore stations. Coho taken within 12 km of shore contained a greater proportion of fishes at two of three stations, while those captured offshore contained more euphausiids.

Chinook Salmon

Thirty taxa were identified from the stomachs of juvenile chinook. Major prey items were juvenile euphausiids (*T. spinifera*), hyperiid amphipods (mostly *Hyperoche medusarum*), pinnotherid crab larvae, and various fishes (Table 3). The most frequently identified fishes were flatfish and Pacific sand lance larvae, both occurring in 31% of the stomachs. Juvenile scorpaenids were third, occurring in only 7% of the stomachs.

Chinook salmon with stomachs full of fresh food ($n = 42$) were studied to test the hypothesis that weight of euphausiids and weight of fish prey in stomachs were independent, using the same procedure as with coho. The χ^2 from the contingency table (Table 7) was significant at the 0.07 level. Hence there is a tendency for chinook to eat either euphausiids or fishes, but this inverse relationship is not as strong as for juvenile coho salmon. The weight of stomach contents increased with size of juvenile chinook salmon. The slope of the regression (weight of prey $= -4.2 + 0.032 \times$ length of chinook, over the range of 100-200 mm) was significantly different from zero ($r = 0.66$, $P<0.05$).

TABLE 7.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 42 juvenile chinook salmon.

		Euphausiid prey (g)	
		= 0.0	>0.0
Fish prey (g)	>0.67	14	7
	<0.67	7	14

Based on the percent by number, euphausiids and fishes were more important in the diet of chinook collected off the Columbia River than off the central Oregon coast (Table 8). As with coho, between-station variability was high. Only three station pairs had high similarities in diet (PSI >90%: 11-12, 11-14, and 12-14) mainly due to the high proportions of *T. spinifera* consumed at these stations.

Diet Overlap

Similarity (PSI) was calculated as before to study diet overlap among species of juvenile salmon at four stations where at least eight individuals of two or more salmon species occurred. Diets were similar (PSI >66%) at three of these stations. At station 12, chum, coho, and chinook juveniles ate 94.7, 93.4, and 90.9% euphausiids, respectively, by number; at station 27, coho and chinook ate nearly equal proportions of hyperiids and fishes; and at station 39, coho and chinook ate 94.0 and 91.3% hyperiids, respectively. Diets were dissimilar at station 1.

This dietary overlap among cooccurring species of juvenile salmonids suggests that a potential exists for competition, should food be limiting. This potential was highest among different size classes of juvenile coho and chinook salmon but was reduced among similar-sized fishes (Fig. 3). Euphausiids were eaten most often by coho 100-200 mm long, but not by chinook <180 mm. The opposite pattern is seen with hyperiid amphipods: Small chinook (<180 mm) ate more hyperiids than similar-sized coho. As juvenile salmonids of both species increased in length, they consumed larger fish, but coho between 140 and 330 mm consumed larger fish on the average than chinook of the same size. Juvenile chinook also consumed more pleuronectid larvae and fewer scorpaenids than coho. Chinook ate very few pteropods and no barnacle cyprids while these taxa occurred in about 10% of the coho stomachs (Table 3).

DISCUSSION

Fishes, euphausiids, hyperiid amphipods, and crab larvae were the most important prey for juvenile salmon off Oregon. Other published studies dealing with the diet of juvenile salmonids in the ocean show basically the same result, although there are notable differences. Manzer (1969) concluded that juvenile chum salmon from Chatham Sound, British Columbia, were planktivorous, feeding mostly on larvaceans (*Oikopleura* spp.) and unidentified copepods, and that coho were piscivorous, feeding mostly on Pacific herring and sand lance. Healey (1980) found that juvenile chum salmon from Saanich Inlet also fed predominantly on larvaceans and copepods, but individuals caught in more open waters of Georgia Strait ate euphausiids, amphipods, and fishes, as found off Oregon in this study. Juvenile coho studied by Healey contained 34% fishes (by volume) in Georgia Strait and 3% in Saanich Inlet, appreciably less than the 70% reported by Manzer in Chatham Sound. Healey concluded that chinook and coho from Georgia Strait had very similar food habits. Fresh et al.

TABLE 8.—Sampling data and percent of total numbers of major prey items found in juvenile chinook stomachs off the Oregon coast (only at those stations where six or more individual chinook were taken). Includes only those prey taxa comprising at least 2% of the total number of prey items.

	Northern Oregon						Central Oregon		
Station	1	8	11	12	14	18	27	39	43
Time of day	0630	1415	1915	0800	1055	1000	0930	0900	0410
Day in June	18	19	19	20	20	21	23	27	28
Water depth (m)	40	38	68	77	71	73	55	55	57
Distance from shore (km)	11.8	11.1	17.2	19.1	18.9	17.6	10.0	9.4	9.3
Number of chinook examined	8	9	12	14	13	14	19	11	6
Average length of chinook (mm)	147	208	239	253	211	245	183	164	178
Percent of chinook with empty or nearly empty stomachs	50	11	8	36	15	29	47	27	17
Thysanoëssa spinifera (juveniles)			97.2	90.9	98.9	22.8			46.4
Hyperiid amphipods		68.1				5.4	37.8	91.3	23.7
Fishes	30.1	25.3		8.3		45.7	19.9		13.4
Crab megalops	2.5	2.1				10.9	7.9	7.5	
Pteropods							31.6		
Euphausia pacifica	61.5								
T. spinifera (adults)	2.5					4.3			
Atylus tridens		2.1				3.2			
Calanus cristatus									12.4
Unidentified items	2.5								
Total number of prey items	39	185	1,906	277	1,846	92	291	987	97

(1981) reported that juvenile chum from nearshore pelagic habitats of Puget Sound fed on euphausiids, crab larvae, and gammarid amphipods on a weight basis; coho fed largely on larvae of decapod crustaceans; and chinook fed on euphausiids.

The qualitative range in variability of diet present during our 2-wk sampling period was similar to that found by the above authors from various months, years, and geographical locations. At some times and locations, euphausiids were dominant prey; at others, amphipods and fishes. This variability suggests that juvenile salmon are opportunistic, feeding on abundant prey available at a particular time and place.

The main prey items of our juvenile salmon comprise three general size groups: 1) Fishes having an average length of 29 mm, 2) euphausiids and *Cancer magister* megalopae, ranging in length from 7 to 10 mm, and 3) hyperiid amphipods between 4 and 6 mm.The fact that juvenile salmonids ate large numbers of euphausiids agrees with what is known about the abundances of various-sized planktonic prey sampled in coastal waters of Oregon during period years (Table 9). Over the range of 7-10 mm, euphausiids were the most abundant prey item. Shrimp larvae and *C. magister* megalopae were abundant only during limited periods, usually only June.

The predominant euphausiid eaten was *T. spinifera*, a neritic species. *Euphausia pacifica*, although a more abundant species of euphausiid in the North Pacific, is more oceanic and is not common in shallow shelf waters (Hebard 1966; Peterson and Miller 1976; Youngbluth 1976) and was found in low numbers in our salmonid stomachs. Juvenile salmonids collected off Oregon fed predominantly on subadult individuals, possibly because adult euphausiids migrate into deeper waters during the day (Alton and Blackburn 1972) when salmon presumably feed. Subadult euphausiids are abundant in the upper 20 m of the water column during both day and night (Peterson[5]).

The large numbers of hyperiid amphipods and the paucity of copepods in the diet of juvenile salmon were surprising. Hyperiids are neither abundant in Oregon coastal waters nor are they particularly large compared with other more common planktonic taxa (Table 9). The average length of the amphipods (4.5 mm) is not much greater than *Calanus marshallae* (stage 5 copepodites and females, 3.0-4.0 mm TL (total length)). The ratio of amphipods to C5 *C. marshallae* abundance was 1:14 in plankton samples (Table 9) but 4:1 in the stomachs of juvenile coho. Frequency of occurrence in juvenile coho stomachs was 44% for amphipods compared with only 6% for *Calanus*. Similarly, the copepod *C. cristatus* (8 mm TL), with an average abundance about the same as hyperiids, was seldom eaten. Length alone may not be adequate for assessing size-selective predation in juvenile salmon. Okada and Taniguchi (1971) found that the upper size limit of prey may be determined by prey width. This may be relevant because hyperiids are generally much broader at their widest dimension than copepods of the same length.

One hypothesis to explain the high selectivity of amphipods by juvenile coho salmon concerns their peculiar swimming behavior and pigmentation. In the laboratory, hyperiids caught in coastal waters were extremely active swimmers (Peterson[6]). Most species have a large, heavily pigmented (black) compound eye, which could increase their detection by a visual predator, as shown for freshwater fish (Zaret and Kerfoot 1975). Copepods, on the other hand, lack the visual contrast of amphipods and are less active swimmers, generally swimming upwards and

TABLE 9.—Abundance of salmonid prey averaged from plankton samples collected during June and July at stations located 1, 3, 5, and 10 mi off Newport, Oreg. Zooplankton are averaged over the years 1969-72 (Peterson and Miller 1976); crab larvae over the years 1969-71 (Lough 1975, 1976); and larval fish from 1971 only (Richardson and Pearcy 1977). Plankton tows are step-oblique through the entire water column, during daytime, using a 0.2 m diameter bongo net (0.24 mm mesh) for zooplankton and a 0.7 m bongo net (0.5 mm mesh) for fish larvae.

Prey taxa	Average no./m³
Pinnotheridae megalopae	0.1-1
Cancer magister megalopae	1-8
Pagurus megalopae	10-20
Calanus cristatus	2.3
C. marshallae (*C5* + females)	50
Pteropods	14.3
Hyperiid amphipods	3.6
Decapod shrimp mysis	19.2
Chaetognaths	11.7
Thysanoëssa spinifera	6.8
Larval fish	1-2

[5]W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, unpubl. data, 1977.

[6]W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, pers. obs. 1978.

then sinking passively through a portion of the water column.

Another explanation for the presence of large numbers of hyperiids in salmonid guts is that juvenile salmon may pick them from the surface of medusae. The predominant hyperiid consumed by chinook and chum salmon was *Hyperoche medusarum*, a species known to live on the exumbrellar surface of medusae (Bowman et al. 1963; Harbison et al. 1977). The host may be easy for salmon to locate, particularly the large *Chrysaora fuscescens* (bell diameter of several tens of centimeters), which were very numerous in our purse seine samples.

Larval fishes were the other important prey item. Information on their distribution and abundance is limited to sampling done in 1971-72. Data given in Table 9 are from Richardson and Pearcy (1977) for larvae captured at stations within 2-28 km from shore. Abundances were 200-400 larvae/10 m^2, or 1-2 larvae/m^3, assuming they are all distributed only within the upper 20 m of the water column.

To investigate the question of food limitation, estimates are needed of salmonid feeding rates, salmonid abundance, prey abundance, and prey population growth rates. Feeding and digestive rates can be inferred from field data, if there is pronounced diel periodicity in stomach fullness or state of digestion (Eggers 1977; Lane et al. 1979), but we have no evidence for this in our limited study. Thus, whereas estimates of stomach fullness were obtained from this study, feeding rates were estimated from other studies. The average weight of food in full juvenile coho stomachs (1.5 g wet weight) is equivalent to about 2.6% of the 55 g body weight of an average juvenile coho (160 mm long) (from Healey 1980). Walters et al. (1978, fig. 6) showed that the maximum ration of juvenile sockeye salmon weighing 55 g is slightly <3% of body weight per day. On the other hand, Brett (1971) found that the maximum daily intake of food was 7-8% of body weight for a 50 g sockeye salmon. Therefore, we assume that juvenile coho fill their stomachs between 1 and 3 times per day on the average.

Averaged over the 2-wk period in June 1979, the average 160 mm juvenile coho contained 37 euphausiids, 28 amphipods, and 4 fish (Table 1). In order to locate this quantity of food, this salmon would have had to search a minimum of approximately 5.4 m^3 of water for the euphausiids, 7.8 m^3 for the amphipods, and at least 4.0 m^3 for the larval fish. This assumes that all prey available to plankton nets are also fully available to juvenile salmon, and that annual differences are minor. Considering the well-known problems of zooplankton sampling variability and the fact that samples from different years are being compared, the agreement on water volume searched by salmon to locate each prey item seems quite good.

The maximum abundance of juvenile salmonids in any one purse seine was 123 fish, and the average number of fish in sets in which at least 5 fish were caught was 26. The mean abundance in these 16 sets was 17 fish/$10^5 m^3$. Juvenile coho abundances were about one-half as great, 8.7 fish/$10^5 m^3$, or 1 fish/11,500 m^3. If a juvenile coho fills its gut once per day, it needs to eat all prey in about 4-8 m^3 water/d. Thus, as a rough average, one individual would consume at least 4/11,500-8/11,500 (or 0.03-0.07%) of the available prey per day. Should this individual coho fill its gut three times each day, it would consume up to 0.1-0.2% of the standing stock of prey per day. Coho and chinook combined would consume about 0.2-0.4% of available prey per day. If growth rates of prey population equal or exceed these loss rates, predation by juvenile coho and chinook alone will not reduce standing stocks of prey. Unfortunately, estimates of these vital parameters are lacking.

Walters et al. (1978) examined the effect of food limitation on juvenile salmon growth and survival using a computer simulation model. Input variables included 1) zooplankton distribution, abundance, and production rates; 2) ration, growth, and mortality of young salmon in relation to body size; and 3) timing of arrival of smolts at sea and rate of migration along the coast in relation to zooplankton production cycles. They tentatively concluded that juvenile salmonids were not food-limited, but rather predator-limited. This conclusion rests on a crucial assumption of the availability of zooplankton prey, which may be in error. Their estimates of zooplankton production and mortality and fish consumption (their table 3, columns 5, 6, and 7) were calculated using estimates of the biomass of zooplankton within a 20-400 m water column, despite their assumption that salmon forage only in the upper 20 m of the water column. They assumed that zooplankton prey removed by salmon during the day will be replaced from deepwater zooplankton populations at night. Since the surface biomass is enhanced by diel vertical migrations mainly at night and juvenile salmonids are thought to be daylight or crepuscular feeders (see Bailey et al. 1975; Godin 1981 and references therein), they may never encounter this nighttime increase in zooplankton abundance.

The studies of Healey (1980) and Simenstad et al. (1980[7]) both suggest that food availability may affect the abundance of juvenile salmon. They found that fewer salmon remained in Georgia Strait (British Columbia) and Hood Canal (Washington), respectively, when feeding conditions were poor. Obviously, the question of ocean limitation of salmon production cannot be resolved until much more is learned about the ecology of juvenile salmon and their competitors in the coastal zone. Substantially more information is needed on the abundance and availability of prey in near-surface waters, as well as on feeding, growth rates, and migration patterns of juvenile salmon.

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LITERATURE CITED

ALTON, M. S., AND C. J. BLACKBURN.
1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58:179-190.

BAILEY, J. E., B. L. WING, AND C. R. MATTSON.
1975. Zooplankton abundance and feeding habits of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fish. Bull., U.S. 73:346-861.

[7]Simenstad, C. A., W. J. Kinney, S. S. Parker, E. O. Salo, J. R. Cordell, and H. Buechner. 1980. Prey community structure and trophic ecology of outmigrating juvenile chum and pink salmon in Hood Canal, Washington. Final rep. (1977-79) No. FRI-UW-8026, 113 p. University of Washington, Fisheries Research Institute, Seattle, WA 98195.

BOWMAN, T. E., C. D. MEYERS, AND S. D. HICKS.
1963. Notes on associations between hyperiid amphipods and medusae in Chesapeake and Narranganset Bays and the Niantic River. Chesapeake Sci. 5:141-146.

BRETT, J. R.
1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28:409-415.

EGGERS, D. M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34:290-294.

FRESH, K. L., R. D. CARDWELL, AND R. R. KOONS.
1981. Food habits of Pacific salmon, baitfish, and their potential competitors and predators in the marine waters of Washington, August 1978 to September 1979. Wash. Dep. Fish. Prog. Rep. 145, 58 p.

GODIN, J.-G. J.
1981. Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Oncorhynchus gorbuscha*) in two marine bays of British Columbia. Can. J. Fish. Aquat. Sci. 38:10-15.

HARBISON, G. R., D. C. BIGGS, AND L. P. MADIN.
1977. The associations of Amphipoda Hyperiidea with gelatinous zooplankton.—II. Associations with Cnidaria, Ctenophora, and Radiolaria. Deep-Sea Res. 24:465-488.

HEALEY, M. C.
1980. The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* W. J. McNeil and D. C. Himsworth (editors), Salmonid ecosystems of the North Pacific, p. 203-229. Oreg. State Univ. Press, Corvallis.

HEBARD, J. F.
1966. Distribution of Euphausiacea and Copepoda off Oregon in relation to oceanographic conditions. Ph.D. Thesis, Oregon State Univ., Corvallis, 85 p.

LANE, E. D., M. C. S. KINGSLEY, AND D. E. THORNTON.
1979. Daily feeding and food conversion efficiency of the diamond turbot: an analysis based on field data. Trans. Am. Fish Soc. 108:530-535.

LOUGH, R. G.
1975. Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Thesis, Oregon State Univ., Corvallis, 229 p.
1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. Fish. Bull., U.S. 74:353-376.

MANZER, J. I.
1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Board Can. 26:2219-2223.

OKADA, S., AND A. TANIGUCHI.
1971. Size relationship between salmon juveniles in shore waters and their prey animals. Bull. Fac. Fish., Hokkaido Univ. 22:30-36.

PETERSON, W., AND C. MILLER.
1976. Zooplankton along the continental shelf off Newport, Oregon, 1969-1972: distribution, abundance, seasonal cycle and year-to-year variations. Oreg. State Univ. Sea Grant College Prog. Publ. ORESU-T-76-002, 111 p.

RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75: 125-145.

WALTERS, C. J., R. HILBORN, R. M. PETERMAN, AND M. J. STALEY.
1978. Model for examining early ocean limitation of Pacific salmon production. J. Fish. Res. Board Can. 35: 1303-1315.

WHITTAKER, R. H.
1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279-338.

YOUNGBLUTH, M.
1976. Vertical distribution and diel migration of euphausiids in the central region of the California Current. Fish. Bull., U.S. 74:925-936.

ZARET, T. M., AND W. C. KERFOOT.
1975. Fish predation on *Bosmina longirostris*: Body-size selection *versus* visibility selection. Ecology 56:232-237.