

Abstract.—First ocean-year feeding habits were determined for juvenile salmon (*Oncorhynchus* spp.) collected with purse seines in marine waters of southeastern Alaska in 1983 and 1984 and northern British Columbia in 1984. Associated prey assemblages were sampled with neuston and plankton nets in 1984. Salmon diets included at least 30 taxa of prey. Crustaceans (principally hyperiid amphipods), fish, and tunicates were the most important prey of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon. Fish were the most important prey of coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon and made up the highest percentage of stomach content weight for all salmon species. Diet shifted from crustaceans in 1983 to fish in 1984 for juvenile pink, sockeye, and chum salmon. Diet overlapped significantly ($\hat{C}_\lambda > 0.60$) between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon. Coho salmon diet overlap was < 0.60 in all paired comparisons. Nearly all (98.6%) of the 2,210 stomachs examined were at least half full. Although, in general, prey consumed were not very similar to prey observed in the environment, the composition of salmon diets was more similar to neuston collections than to zooplankton collections.

Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia

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All Pacific salmon (*Oncorhynchus* spp.) migrate as juveniles from shallow waters near shore to coastal and oceanic feeding areas of the North Pacific Ocean, where species, stocks, and age classes mix (Hartt and Dell, 1986; Ware and McFarlane, 1989; Percy, 1992). Substantial evidence suggests that salmon production around the Gulf of Alaska increased dramatically in the late 1970's, possibly owing to enhanced early ocean survival (Percy, 1992; Beamish and Bouillon, 1993; Brodeur and Ware, 1995). Increased densities are evident in the commercial harvest of salmon in Alaska; for example, salmon catch reached record numbers in 1993, nearly doubling over 25 years to approach 200 million fish (Wertheimer, 1997). This increase is attributed to several factors, including growing enhancement efforts and environmental conditions that favor survival of both wild and hatchery salmon stocks.

The increase in numbers of subadult and adult salmon feeding in marine waters has prompted interest in possible density-dependent effects on survival, growth, and production of salmon stocks around the

Pacific rim (e.g. Helle, 1989; Kaeriyama, 1989; Ishida et al., 1993; Helle and Hoffman, 1995). Fishery managers are concerned about the effects of increasing interactions between salmon populations—both wild and enhanced—in the various marine habitats where they mature (McNeil and Himsforth, 1980; Peterson et al., 1982; Brodeur, 1989; Brodeur and Percy, 1990; Percy, 1992). The feeding ecology of juvenile salmon is a pertinent, but not well known, topic.

The objective of this study was to describe the feeding habits of juvenile salmon during their first summer in coastal waters of the eastern Gulf of Alaska. Although Hartt and Dell (1986) summarized the distribution, migration, and growth of juvenile salmon in the North Pacific Ocean and the Bering Sea, diet and feeding were addressed superficially. Other references concerning juvenile salmon feeding habits during early marine residence, especially along the open coast, are limited (Percy, 1992; Brodeur¹), and juvenile salmon diets are often

treated as a subset of adult diets (e.g. Groot and Margolis, 1991). Therefore, as a first step to understanding trophic interactions during their first marine summer, our research focused on the feeding habits and diet overlap of juvenile chinook (*O. tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon. We compared diet overlap between species, habitats, months, and years and also examined the similarity of salmon diets with samples of prey collected concurrently.

Methods

Fish collection

Juvenile salmon were collected in 120 purse-seine sets made along transects with two vessels and two seines (Table 1; see also Jaenicke and Celewycz, 1994). The 28-m NOAA RV *John N. Cobb* fished a table seine in the marine waters of southeastern Alaska during August 1983 and July and August 1984 (Fig. 1). The 24-m FV *Bering Sea* fished a drum seine in the open coastal waters of northern British Columbia during July 1984. Purse-seine sets at all locations were standardized to compensate for different sizes, meshes, and areas enclosed; both nets had 25-mm mesh in the bunt (Jaenicke and Celewycz, 1994). Each station was fished only once during a period, except on a few occasions when a set was repeated following an empty haul. Fishing was conducted almost exclusively between 0600 and 1800 hours. All sets were round hauls (i.e. the seine was not towed or held open to increase catches). The distribution, size, and abundance of juvenile salmon examined for our study have been summarized in a companion paper by Jaenicke and Celewycz (1994).

The waters sampled were partitioned into discrete habitats: 1) outside waters: the open waters adjacent to the Gulf of Alaska; 2) inside waters: the enclosed marine waters of the Alexander Archipelago; and 3) protected outer-coast inlets (Fig. 1). Outside waters were further partitioned into nearshore (0–37 km offshore) and offshore (46–74 km offshore) during August 1984; seining was restricted to within 37 km of shore during other sampling periods. Inside waters were partitioned into bays and passages (connecting to the Gulf of Alaska). Sampling in outside

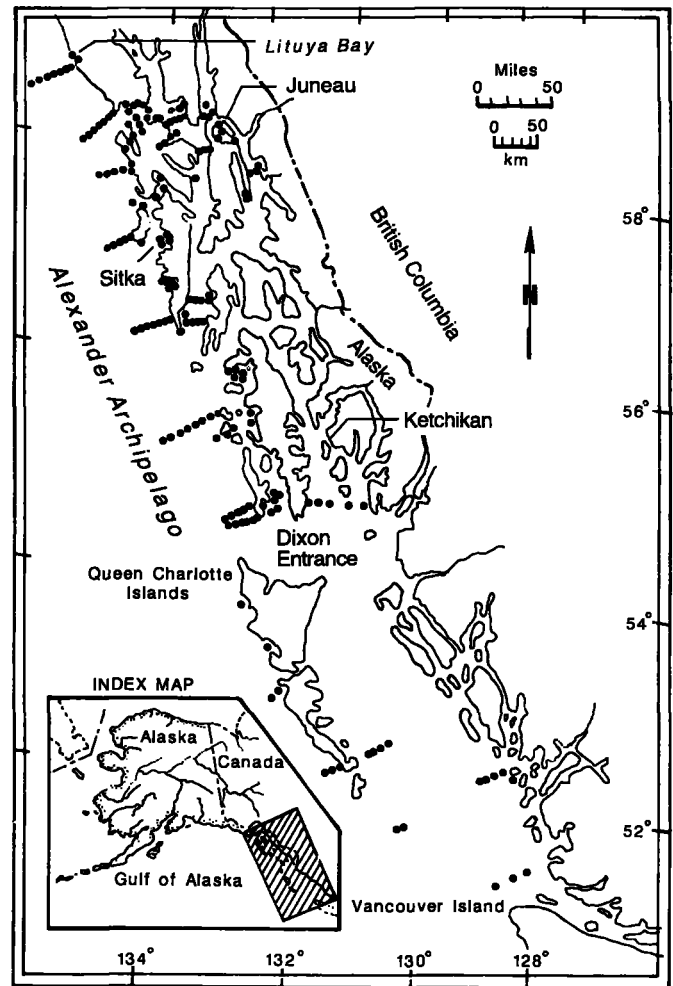


Figure 1

Location of purse-seine sets in southeastern Alaska in 1983 and 1984 and in British Columbia in 1984.

waters was along transects about 72 km apart in southeastern Alaska and 108 km apart in British Columbia. Transects began as close to shore as submarine topography and seine depth permitted and continued up to 74 km offshore, depending on fish abundance and weather.

Fish from each purse-seine haul were anesthetized with MS 222 (tricaine methanesulfonate), sorted, identified, and measured on board the vessel. A subsample of each salmon species ($n \leq 25$) was preserved in 10% formalin-seawater solution for later stomach analysis (Table 1). Nonsalmonids caught incidentally were identified and enumerated, catch per unit of effort (CPUE) was estimated, and a subsample was measured for length as part of prey assemblage assessments (see below). Sea surface temperature (SST) to the nearest 0.2°C was recorded at every purse-seine site.

¹ Brodeur, R. D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific (INPFC Doc.) FRI-UW-9016. Fish. Res. Inst., Univ. Washington, Seattle, 38 p.

Table 1

Number of purse-seine sets by time period and habitat and subsample size by species of juvenile salmon used in diet analyses. BC = British Columbia; AK = Alaska.

Habitat	Number of sets	Number of sets catching juvenile salmon	Number of fish				
			Pink	Chum	Sockeye	Coho	Chinook
August 1983							
Inside inlet	15	3	21	23	2	14	1
Inside passage	39	23	142	112	44	88	2
Outer coast inlet	27	8	60	47	0	21	0
Outside waters	8	4	15	2	9	26	0
Total	89	38	238	184	55	149	3
July 1984							
Inside inlet	13	5	14	17	12	63	10
Inside passage	5	2	20	3	9	44	0
Outer coast inlet	14	5	8	3	0	28	0
Outside waters (BC)	21	11	69	30	55	7	3
Outside waters (AK)	33	15	94	40	83	27	1
Total	86	38	205	93	159	169	14
August 1984							
Inside inlet	18	6	35	16	10	82	6
Inside passage	19	7	61	10	5	73	10
Outer coast inlet	4	1	0	12	0	3	0
Outside nearshore	26	20	183	97	80	55	5
Outside offshore	11	10	93	41	52	12	0
Total	78	44	372	176	147	225	21
All periods combined							
Inside inlet	46	14	70	56	24	159	17
Inside passage	63	32	223	125	58	205	12
Outer coast inlet	45	14	68	62	0	52	0
Outside waters	99	60	454	210	279	127	9
Total	253	120	815	453	361	543	38

Stomach analysis

Each fish was weighed to the nearest milligram and measured to the nearest millimeter fork length (FL) in the laboratory. Stomachs were excised and placed in 70% isopropyl alcohol. During analysis, stomach fullness on a scale of 0–6 (0=empty, 6=distended) and digestion on a scale of 1–4 (1=fresh prey items, 4=completely digested) were visually estimated. Stomach contents were weighed, and prey items were separated, identified to the lowest convenient taxon, and counted. Up to 100 individuals of each prey category that had been removed in good condition from the stomach were used to measure initial wet weights. Prey fish in an advanced state of digestion were assigned to discrete weight categories based on the most complete specimens encountered: small (estimated 6.0 mg), medium (184.4 mg), and large (580.5 mg). Dry weights were obtained by drying the samples in an oven at 60°C until constant weights were obtained.

Sampling and analysis of prey assemblages

Prey assemblages were sampled with neuston and plankton nets in the areas fished in 1984. Neuston collections were made with a rectangular 100 × 35-cm-opening neuston-net frame containing a conical 505-µm-mesh net; tows were made at 45 of 54 outside-water locations, 7 of 14 outer-coast-inlet locations, and 5 of 18 inside-water locations. The neuston net was towed horizontally, half-submerged, so that it sampled the water column from the surface to approximately 17 cm depth (Brodeur, 1989; Brodeur²). The plankton collections were made with a 70-cm diameter conical plankton net of 303-µm mesh; tows were made along purse-seine transects at four 4-km locations and six 16-km locations in

² Brodeur, R. D., W. G. Pearcy, B. C. Mundy, and R. W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution, and utilization by juvenile salmonids. Oregon State Univ. Publ. ORESU-T-87-001, 61 p.

outside waters, and at six locations in inside waters. All plankton tows were oblique from the surface to a depth of 50 m. Samples were preserved in a 10%-formalin-seawater solution after debris was removed.

Plankton and neuston samples were sorted to remove large organisms, such as gelatinous zooplankton. We then split the sample with a Folsom splitter until a subsample of about 500 organisms remained. Plankton organisms were identified to the lowest convenient taxon and counted. Detailed composition of many of the neuston samples has been presented elsewhere (Brodeur²).

Data analysis

Stomach data were partitioned into subsets according to salmon species, geographic area, habitat, distance offshore, month, and year. The index of relative importance (IRI; Pinkas et al., 1971) was calculated for each data subset. The modified IRI (dry weight rather than volume) was used to characterize the diet of each species and to rank prey taxa:

$$IRI = (N + W)F,$$

where N is numerical percentage, W is weight percentage, and F is frequency of occurrence (FO) percentage. In all comparisons, the IRI is expressed as a percentage of total IRI for each data subset.

Morisita's index of overlap as modified by Horn (1966) was used to calculate overlap between species pairs; values range from 0 (no overlap) to 1 (complete overlap):

$$\hat{C}_\lambda = \frac{2 \sum_{i=1}^S x_i y_i}{\sum_{i=1}^S x_i^2 + \sum_{i=1}^S y_i^2},$$

where x_i and y_i are proportions of the numbers of individuals of prey species i found in the predator species x and y , respectively.

The percent similarity index (PSI; Whittaker, 1975) was used to compare stomach samples to plankton samples:

$$PSI = \sum \min(p_a \text{ or } p_b),$$

where p_a is percentage number for a given species in sample A, and p_b is percentage number for the same species in sample B. A PSI value of 1.00 shows complete similarity; a value of 0 indicates no similarity. We considered values ≥ 0.60 to be significant for both overlap indices. Chinook salmon were not included

in the analysis of overlap because of small sample sizes (Table 1). Following Brodeur and Pearcy (1990), we tested for differences in the occurrence of principal prey between years, months, areas, and distance offshore using χ^2 .

We examined data for neuston and plankton prey samples collected at locations where stomachs of at least five specimens of one salmon species were available and included a taxon in the prey collections. To measure prey selection, we used Strauss's linear food selection index (Strauss, 1979):

$$L = r_i - p_i,$$

where r_i and p_i are the proportional abundances of prey item i in the gut and habitat, respectively. Selection values range from -1 , indicating avoidance or negative accessibility, to $+1$, indicating preference or positive selection; 0 indicates random feeding. Values are extreme only when the prey item is proportionately abundant but rarely consumed (-1), or is proportionately rare but consumed almost exclusively ($+1$). We tabulated selection values >0.10 or <-0.10 for an indication of the positive or negative selection of a particular taxon.

To compare the number of stomachs required to characterize the breadth of diet for each species of salmon, we pooled the stomachs over all periods and habitats. Stomachs were selected randomly, and the cumulative number of taxa were plotted versus the number of stomachs until the asymptote was reached (Hurtubia, 1973).

Results

Description of diet

All salmon species The prey spectrum for juveniles of five Pacific salmon species comprised at least 30 taxa (Table 2). The six taxonomic groups of greatest importance (IRI) were calanoid copepods, hyperiid amphipods, euphausiids, decapods, tunicates, and fishes (Table 3). In pooled samples, fish were the most important prey for coho and chinook salmon (IRI=63.8% and 76.4%) but were only moderately important for the other species (IRI 28.3–40.3%). Hyperiid amphipods, most commonly *Themisto* spp., were also important prey for pink, chum, and sockeye salmon (IRI 28.0–39.6%). However, the biomass of teleost prey made up more than 75% of the total biomass consumed by each of the juvenile salmon species in pooled samples.

The full breadth of the prey spectrum for juvenile salmon species was obtained by randomly selecting

16–95% of the actual number of stomachs analyzed (Fig. 2). The highest cumulative numbers of prey taxa ($n=25$ and 26 , respectively) were observed after we had randomly subsampled 86 coho and 396 pink salmon stomachs (Fig. 3). Virtually all chinook salmon analyzed (39) were needed to reach the 14 cumulative prey taxa observed. The curves of cumulative number of taxa for pink and chum salmon were more similar than for any other pair of species (Fig. 3).

Pink salmon The prey of juvenile pink salmon (85–222 mm FL; $\bar{x}=142$ mm; $SD=22.9$) encompassed 26 taxa and several life-history stages. Hyperiid amphipods, especially the genus *Themisto*, had the highest total IRI (Fig. 4) and highest FO and mean abundance over all periods and habitats (Table 3). Juvenile fish had the second-highest IRI and the greatest biomass—76% of pooled weight of stomach contents. In 1984, the IRI for fish prey did not rank first, but it was more than twice the 1983 value; fish prey ranked higher in Alaska than in British Columbia. Tunicates, primarily the larvacean *Oikopleura dioica*, were the third most important prey in pooled samples.

Chum salmon The prey spectrum for juvenile chum salmon (80–276 mm FL; $\bar{x}=151$ mm; $SD=28.4$) included 22 taxonomic groups and several life-history stages. Juvenile fish, tunicates (salps and the larvacean *O. dioica*), and hyperiid amphipods (*Themisto* spp.) had the highest IRI's overall (Fig. 5).

Sockeye salmon The prey spectrum for juvenile sockeye salmon (91–202 mm FL; $\bar{x}=151$ mm; $SD=18.9$) encompassed 18 taxonomic groups and several life-history stages. Fish prey had the highest IRI (40.3%) and the greatest average weight (87.2%) pooled over all habitats and periods (Table 3; Fig. 6), although no fish were sampled from outer-coast inlets (Table 1). Fish prey were more important in 1984 than in 1983, especially in the outside waters of southeastern Alaska in July 1984 and inside inlets and outside waters (>37 km) in August 1984 (Fig. 6). Hyperiid amphipods (*Themisto* spp.) were the second

Table 2

Prey from juvenile salmon stomachs as index of relative importance (IRI). $IRI = (N + W)FO$, where N = numerical percentage, W = weight percentage, and FO = frequency of occurrence percentage. Numbers in parentheses are totals of taxonomic groups for which more than one taxon is listed.

Prey	IRI (%)				
	Pink	Chum	Sockeye	Coho	Chinook
Polychaeta					
Unidentified	<0.01	<0.01	—	<0.01	<0.01
Mollusca	(0.90)	(0.16)	(0.17)	(0.02)	(—)
Gastropoda					
<i>Limacina helicina</i>	0.82	0.16	0.15	0.02	—
Bivalvia					
Unidentified	<0.01	<0.01	—	—	—
Cephalopoda					
Unidentified	0.08	<0.01	0.02	<0.01	0.18
Copepoda	(3.71)	(2.93)	(4.15)	(0.02)	(<0.01)
<i>Neocalanus cristatus</i>	<0.01	—	—	—	—
<i>Epilabidocera longipedata</i>	<0.01	—	<0.01	—	—
Unidentified	3.70	2.93	4.14	0.02	<0.01
Cumacea					
Unidentified	<0.01	<0.01	—	—	—
Amphipoda					
Hyperideia	(39.61)	(28.03)	(36.48)	(6.84)	(0.10)
<i>Hyperia</i> sp.	0.01	0.01	0.01	0.02	0.01
<i>Themisto</i> spp.	38.75	27.44	36.11	6.73	0.08
<i>Primno macropa</i>	0.83	0.58	0.36	0.09	0.01
<i>Vibilia</i> sp.	0.02	<0.01	0.01	<0.01	—
Euphausiacea	(5.95)	(6.18)	(12.62)	(3.88)	(18.34)
<i>Euphausia pacifica</i>	<0.01	—	—	<0.01	—
<i>Thysanoessa spinifera</i>	<0.01	0.01	—	0.01	0.08
Unidentified	5.94	6.17	12.62	3.86	18.26
Decapoda					
Unidentified	4.67	3.16	3.64	25.26	4.81
Insecta					
Unidentified	0.01	<0.01	<0.01	0.01	—
Chaetognatha					
Unidentified	0.01	0.01	<0.01	<0.01	—
Urochordata					
(tunicates)	(13.56)	(30.32)	(2.26)	(0.03)	—
Salpidae					
Unidentified	<0.01	0.21	—	<0.01	—
Larvacea					
<i>Oikopleura dioica</i>	13.56	30.11	2.26	0.03	—
Osteichthyes	(31.11)	(29.88)	(40.27)	(63.78)	(76.42)
<i>Clupea pallasii</i>	—	—	—	0.01	0.26
Osmeridae	<0.01	0.02	—	<0.01	0.61
Myctophidae	0.02	0.02	<0.01	—	—
<i>Theragra chalcogramma</i>	—	—	—	0.01	—
<i>Sebastes</i> spp.	0.04	—	0.03	0.04	—
Cottidae	—	—	—	<0.01	—
Stichaeidae	<0.01	—	<0.01	<0.01	0.02
<i>Ammodytes hexapterus</i>	<0.01	0.03	—	0.30	0.47
Pleuronectidae	—	<0.01	<0.01	0.02	—
Unidentified	31.04	29.80	40.22	63.39	75.06

Table 3

Stomach contents of juvenile salmon in marine waters of southeastern Alaska and northern British Columbia in 1983 and 1984. *N* is numerical percentage, *W* is dry weight percentage, *FO* is frequency of occurrence percentage of fish with prey item *i*, and *IRI* is percent of total IRI for all prey taxa. $IRI = (N + W)FO$. Taxa are omitted if IRI is $\leq 1\%$ for all salmon.

	Pink salmon				Chum salmon				Sockeye salmon				Coho salmon				Chinook salmon			
	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)	N (%)	W (%)	FO (%)	IRI (%)
All periods combined																				
Calanoids	5.6	0.9	47.9	3.7	5.4	0.8	32.9	3.0	9.0	0.5	41.5	4.2	—	—	—	—	—	—	—	—
Decapods	3.8	4.0	48.6	4.7	2.4	3.6	36.6	3.1	5.4	2.6	43.2	3.6	52.0	0.1	56.3	25.3	11.2	0.2	38.5	4.8
Euphausiids	5.2	5.5	46.2	6.0	6.0	5.9	39.8	6.1	16.5	4.3	57.4	12.6	12.8	0.1	35.8	3.9	52.6	0.2	33.3	18.3
Hyperiid	45.2	5.8	90.3	39.6	29.5	5.7	73.6	28.0	46.2	3.7	90.1	36.5	22.9	0.1	46.4	6.8	1.5	0.2	7.7	0.1
Tunicates	32.2	0.1	35.2	13.6	52.5	0.1	46.7	30.1	16.4	<0.1	13.1	2.3	—	—	—	—	—	—	—	—
Teleosts	1.3	76.0	39.1	31.2	0.9	82.7	28.6	28.3	2.9	87.2	47.0	40.3	8.4	99.5	73.2	63.8	30.2	99.0	71.8	76.4
Total	93.3	92.3		98.8	96.7	98.7		98.6	96.4	98.3		99.5	96.1		99.8	99.8	95.5		99.5	99.6
August 1983																				
Calanoids	6.4	2.9	62.6	6.6	2.0	4.7	39.7	3.1	10.9	4.6	52.7	6.0	0.4	<0.1	10.1	<0.1	—	—	—	—
Decapods	4.3	8.6	60.9	8.9	0.9	12.1	32.6	4.8	1.1	8.3	30.9	2.2	46.4	0.5	63.1	26.4	—	—	—	—
Euphausiids	4.9	14.1	52.9	11.4	5.3	32.7	46.2	18.4	17.0	39.0	76.4	31.5	5.8	0.6	36.9	2.0	—	—	—	—
Hyperiid	37.0	12.4	71.0	33.6	31.5	28.0	64.7	38.5	58.5	30.7	94.5	55.1	41.5	0.6	59.7	21.7	—	—	—	—
Tunicates	38.7	0.2	48.7	20.3	56.8	0.5	60.9	28.8	8.7	0.1	14.5	0.9	0.1	<0.1	6.0	<0.1	—	—	—	—
Teleosts	0.4	56.7	29.9	16.6	0.2	20.2	19.6	4.6	0.3	16.7	21.8	2.7	2.7	96.4	61.1	49.1	—	—	—	—
Total	91.7	94.9		97.4	96.7	98.2		98.2	96.5	99.4		98.4	96.9		98.1	99.2	—	—	—	—
July 1984																				
Calanoids	15.0	0.8	39.0	7.3	23.4	1.4	28.0	11.0	12.1	0.4	4.3	5.6	0.7	<0.1	7.1	<0.1	—	—	—	—
Decapods	4.7	1.9	42.0	3.3	1.1	2.1	26.9	1.4	8.8	0.8	32.1	3.2	54.3	0.1	65.7	27.6	—	—	—	—
Euphausiids	7.0	5.0	46.3	6.6	4.8	8.1	37.6	7.7	23.0	3.4	62.3	17.0	16.6	0.1	33.7	3.8	—	—	—	—
Hyperiid	45.2	4.3	68.3	39.4	26.0	6.3	53.8	27.1	37.8	2.0	70.4	28.9	6.1	0.1	25.4	0.8	—	—	—	—
Tunicates	11.9	<0.1	17.6	2.5	34.3	0.1	29.0	15.8	9.1	<0.1	7.5	0.7	4.1	<0.1	5.3	<0.1	—	—	—	—
Teleosts	3.6	84.2	39.0	38.4	3.9	77.4	32.3	35.0	4.2	92.0	45.9	43.9	15.5	99.7	84.0	67.6	—	—	—	—
Total	87.4	96.2		97.5	93.5	95.4		98.0	95.0	98.6		99.3	97.3		100	99.8	—	—	—	—
August 1984																				
Calanoids	2.3	0.7	37.9	1.3	3.8	0.3	25.1	1.5	4.7	0.5	32.7	1.8	0.2	<0.1	2.7	<0.1	—	—	—	—
Decapods	3.2	3.9	43.4	3.7	5.0	2.9	42.9	5.0	4.5	5.3	61.2	6.4	58.3	0.1	42.7	24.7	—	—	—	—
Euphausiids	4.8	3.7	39.3	3.9	7.3	2.4	29.7	4.2	9.6	3.8	41.5	5.9	19.7	0.1	32.4	6.3	—	—	—	—
Hyperiid	50.1	5.0	65.3	40.8	27.9	3.0	53.1	22.6	47.5	5.1	68.7	36.5	10.3	0.1	24.0	2.1	—	—	—	—
Tunicates	34.4	<0.1	34.7	14.4	52.8	<0.1	37.1	28.9	28.3	<0.1	19.7	5.9	<0.1	<0.1	0.1	<0.1	—	—	—	—
Teleosts	1.1	85.1	38.5	35.5	0.8	90.8	28.0	37.3	3.1	83.1	47.6	43.4	10.7	99.6	72.9	66.8	—	—	—	—
Total	95.9	98.4		99.6	97.6	99.4		99.5	97.7	97.8		99.9	99.2		99.9	99.9	—	—	—	—

most important prey group (IRI=36.5%) and had the highest FO and average count (Table 3).

Coho salmon The prey spectrum of juvenile coho salmon (112–309 mm FL; \bar{x} =222 mm; SD=35.1) encompassed 25 taxonomic groups, including eight identifiable fish families (Table 2). Teleosts made up 99.5% of the total prey weight, with a mean number of 8.4 fish consumed by 73.2% of the coho predators (Table 3). Juvenile fishes were the principal component of coho salmon diet in all habitats except in the outside waters during August 1983 (Fig. 7), when decapod larvae were more important (IRI=66%). The IRI for prey fish ranged from 51% to 81% in the other habitats, with Pacific sand lance (*Ammodytes hexapterus*) the most prevalent species. Other iden-

tifiable prey fish (in order of importance) included walleye pollock (*Theragra chalcogramma*), rockfish (*Sebastes* spp.), flatfish (Pleuronectidae), Pacific herring (*Clupea pallasii*), smelt (Osmeridae), pricklebacks (Stichaeidae), and sculpins (Cottidae). Fish were more important in 1984 than in 1983 and higher in Alaska than in British Columbia.

Chinook salmon The prey spectrum of juvenile chinook salmon (139–324 mm FL; \bar{x} =224 mm; SD=58.4) encompassed 14 taxonomic categories and four identifiable fish families (Table 2). Fish were the most important prey: IRI's ranged from 28% to 100% among habitats (data not shown). Fish made up 99% (biomass) of chinook salmon stomach contents in pooled samples, with a mean of 30.2 individuals con-

sumed by approximately 72% of the predators (Table 3). Identifiable fish (in order of importance) included smelt, Pacific sand lance, Pacific herring, and pricklebacks. Euphausiids were an important prey principally in inside inlets during July 1984. Incidental prey included decapod larvae, squid, and hyperiid amphipods.

Variation in principal prey

Diets of all four species varied greatly (Table 4). Variation in the FO of the six principal prey (calanoids, decapod larvae, euphausiids, fish, hyperiid amphipods, and tunicates) was greatest when compared between years: the FO of most invertebrate taxa decreased significantly ($P \leq 0.05$) in the diets from August 1983 to August 1984, whereas the FO of teleost prey increased (Tables 3 and 4). Except for coho salmon, variation in the FO of fish was greatest for inshore-offshore comparisons; significantly more fish were consumed by the other species offshore (>37 km from the coast) than inshore (0–37 km from the coast) (Table 4; $12.69 < \chi^2 < 47.72$; $P \leq 0.001$). In 1984, the FO of two principal prey taxa differed consistently in opposite directions between areas: pink, chum, and sockeye salmon ate teleost prey significantly less often ($6.94 < \chi^2 < 13.42$; $P \leq 0.01$), whereas all four species consumed euphausiids significantly more often ($5.66 < \chi^2 < 17.13$; $P \leq 0.05$) in British Columbia waters than in Alaska. The diet of sockeye salmon varied more than that of the other species between years (August 1983 and August 1984), months (July and August), and areas (British Columbia and southeastern Alaska; Table 4).

Diet overlap

Samples pooled over time and habitat Significant diet overlap ($\hat{C}_\lambda > 0.60$) was found between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon when all samples were pooled. Coho salmon diet overlap was less than 0.60 in all comparisons. Diet overlap was not

calculated for chinook salmon because of small sample sizes (Table 1). The greatest diet overlap was between pink and sockeye salmon juveniles ($\hat{C}_\lambda = 0.93$; Table 5); both species ate fish and hyperiid amphipods. The second-greatest diet overlap ($\hat{C}_\lambda = 0.91$) was between pink

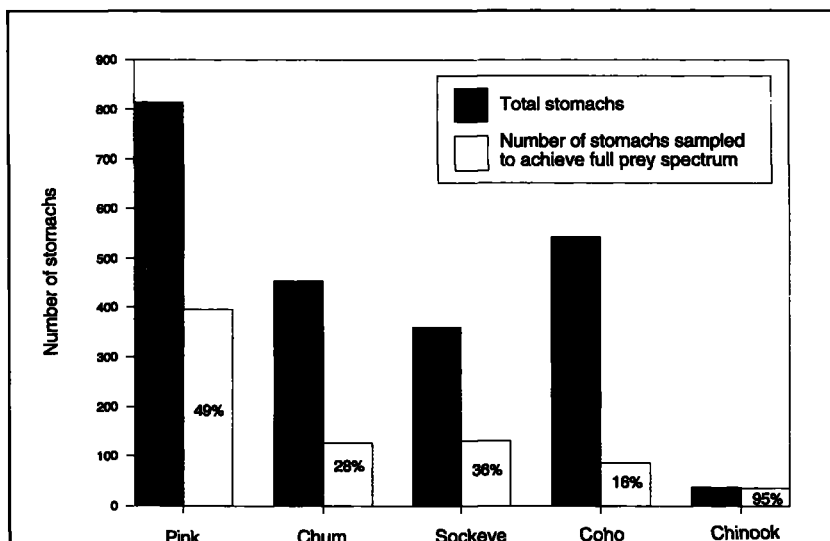


Figure 2

Total number of stomachs sampled for five species of juvenile Pacific salmon and number and percentage of randomly selected stomachs, from samples pooled over habitats and time periods, which were required to achieve the full prey spectrum for each species as defined in this study.

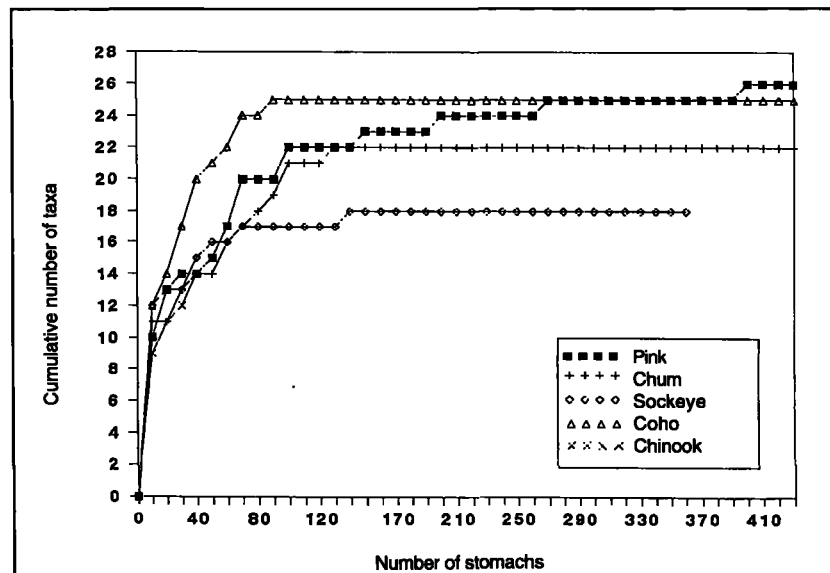
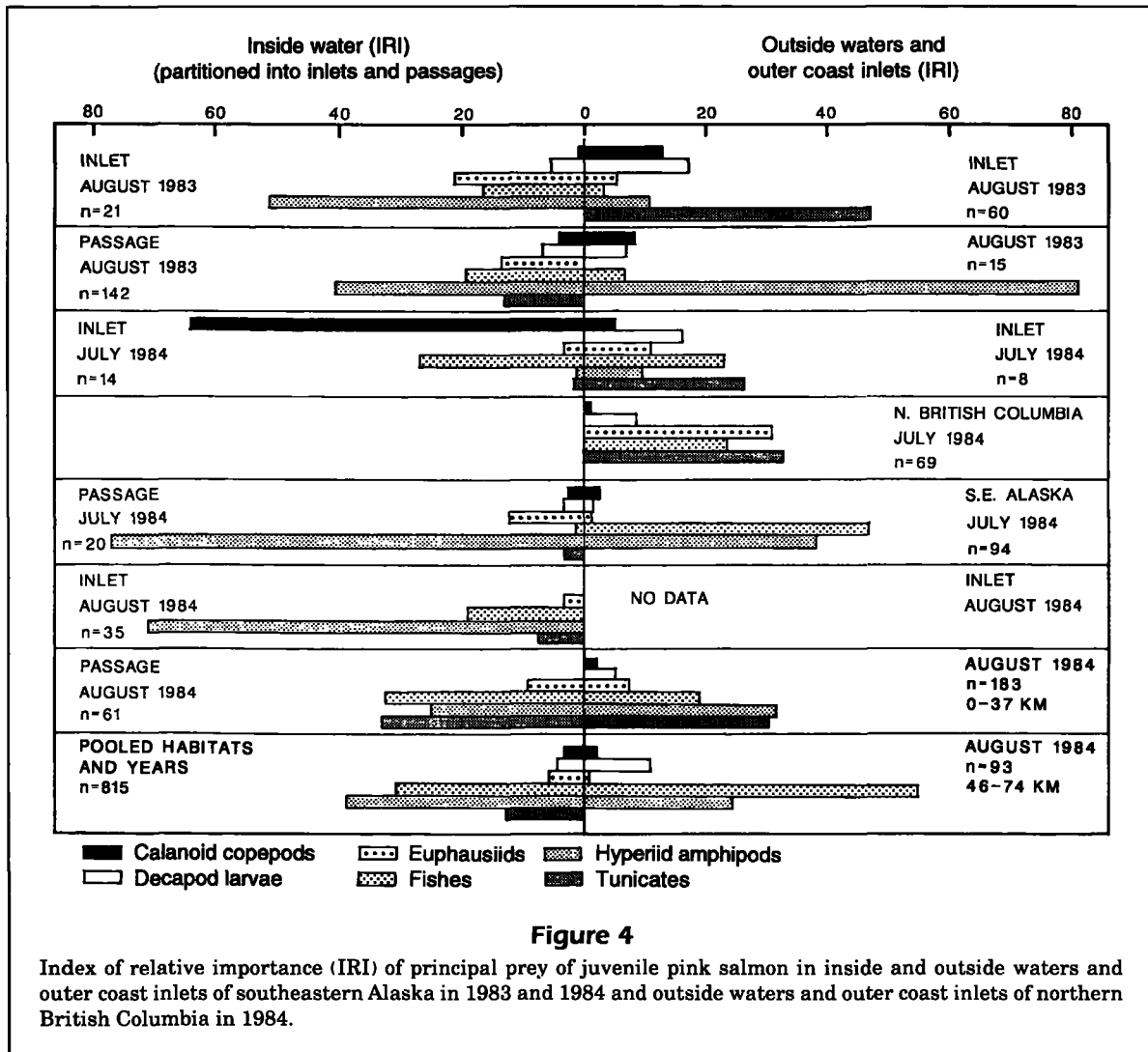


Figure 3

Curves of cumulative number of prey taxa versus pooled number of fish examined from five Pacific salmon species in marine waters of southeastern Alaska and northern British Columbia.

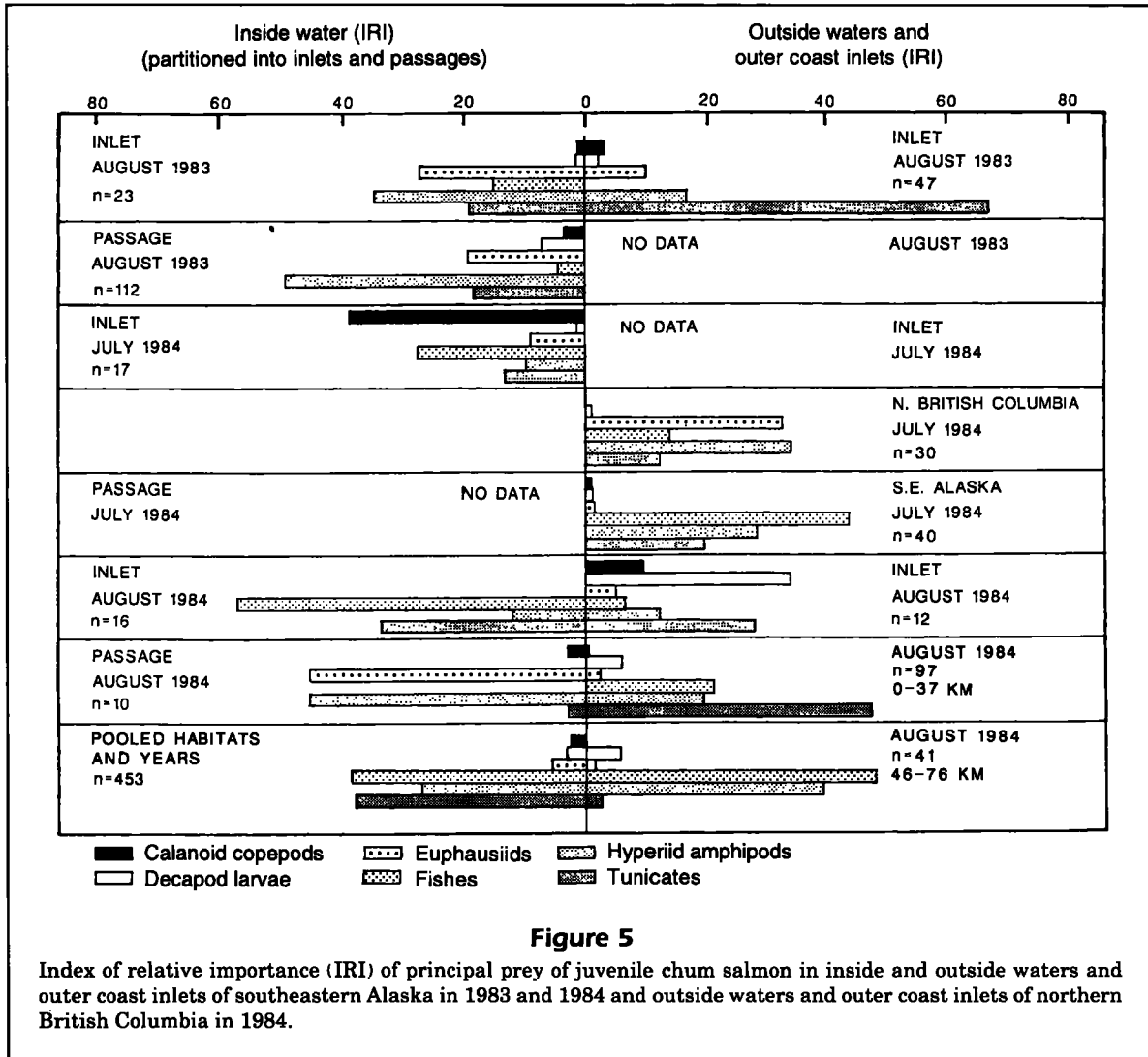


and chum salmon; both ate hyperiid amphipods, fish, and *Oikopleura dioica*. The third-highest diet overlap in all pooled samples was between chum and sockeye salmon ($\hat{C}_\lambda = 0.73$); both species consumed fish, hyperiid amphipods, and euphausiids.

Temporal diet overlap The degree of diet overlap among salmon species pairs varied by time period when habitat was not considered. In August 1983, diet overlap, based on the consumption of hyperiid amphipods, was greatest for pink and chum salmon juveniles ($\hat{C}_\lambda = 0.95$; Table 5), *O. dioica*, and euphausiids. Diets of juvenile pink and sockeye salmon overlapped significantly ($\hat{C}_\lambda = 0.72$) on the basis of hyperiid amphipods and euphausiids. A lesser, but still significant, diet overlap ($\hat{C}_\lambda = 0.62$) occurred between sockeye and coho salmon on the basis of hyperiid amphipods, decapod larvae, and fish.

Diet overlap was lower in July 1984, when samples included waters outside of British Columbia, than in August 1984. Diet overlap was significant for combinations of pink, chum, and sockeye salmon, but not for combinations including coho salmon (Table 5). The greatest overlap occurred between pink and chum salmon ($\hat{C}_\lambda = 0.80$), pink and sockeye salmon ($\hat{C}_\lambda = 0.79$), and chum and sockeye salmon ($\hat{C}_\lambda = 0.73$), which was principally due to similar proportions of hyperiid amphipods and juvenile fish. The relative importance of larvaceans accounted for the greatest difference in the diets of these three species: *O. dioica* made up nearly 20% of the IRI for chum salmon, compared with less than 3% for pink and sockeye salmon.

In August 1984, the diets of pink, sockeye, and chum salmon overlapped greatly, whereas coho salmon diet did not overlap with that of any other species (Table 5). Diets of pink and sockeye salmon overlapped almost



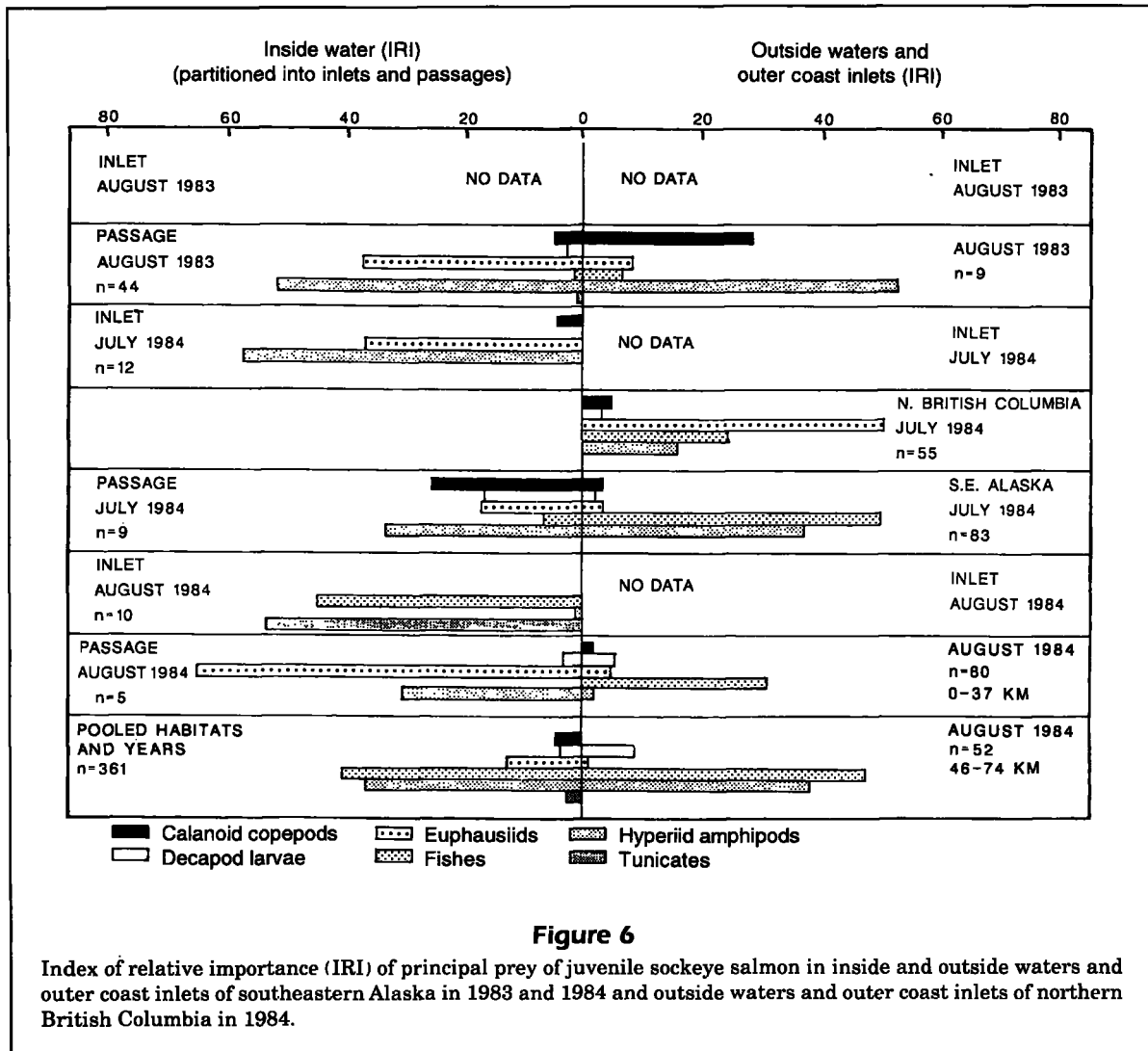
completely ($\hat{C}_\lambda = 0.99$); prey composition and IRI for each prey category were highly similar (Table 2). Pink and chum salmon diets ($\hat{C}_\lambda = 0.88$) and sockeye and chum salmon diets ($\hat{C}_\lambda = 0.85$) had almost identical prey species compositions, although proportions of prey categories differed (Table 2).

Spatial diet overlap Diet overlap was more common for species comparisons in outside waters than in inside waters. Of all possible habitat comparisons, diet overlap was significant ($\hat{C}_\lambda \geq 0.60$) in 42% of the outside-waters comparisons, 39% of inside-passage comparisons, and 29% of inside-inlet comparisons (Table 5). Within each habitat, mean overlap (all periods) was significant in inside inlets for pink and chum salmon ($\hat{C}_\lambda = 0.66$), inside passages for pink and chum salmon ($\hat{C}_\lambda = 0.91$), and chum and sockeye salmon ($\hat{C}_\lambda = 0.73$), and outside waters for pink and

sockeye salmon ($\hat{C}_\lambda = 0.83$), chum and sockeye salmon ($\hat{C}_\lambda = 0.68$), and pink and chum salmon ($\hat{C}_\lambda = 0.67$).

Fullness and digestion

Most salmon stomachs were evaluated to be at least half full (fullness index of 3); coho salmon stomachs were more full than those of other species (Table 6). Stomach fullness was always greater for fish from the inside waters than from outside waters; stomachs of fish caught 0–37 km offshore were less full than those of fish caught >37 km offshore. Only 32 of 2,210 (1.4%) stomachs sampled were empty: 72% in outside waters, 3% in coastal inlets, and 25% in inside waters. The contents of most stomachs were “partly digested” (digestion index of 2). Pink, chum, and coho salmon from inside waters had stomach contents in an earlier stage of digestion than fish



from outside waters; the reverse was observed for sockeye salmon.

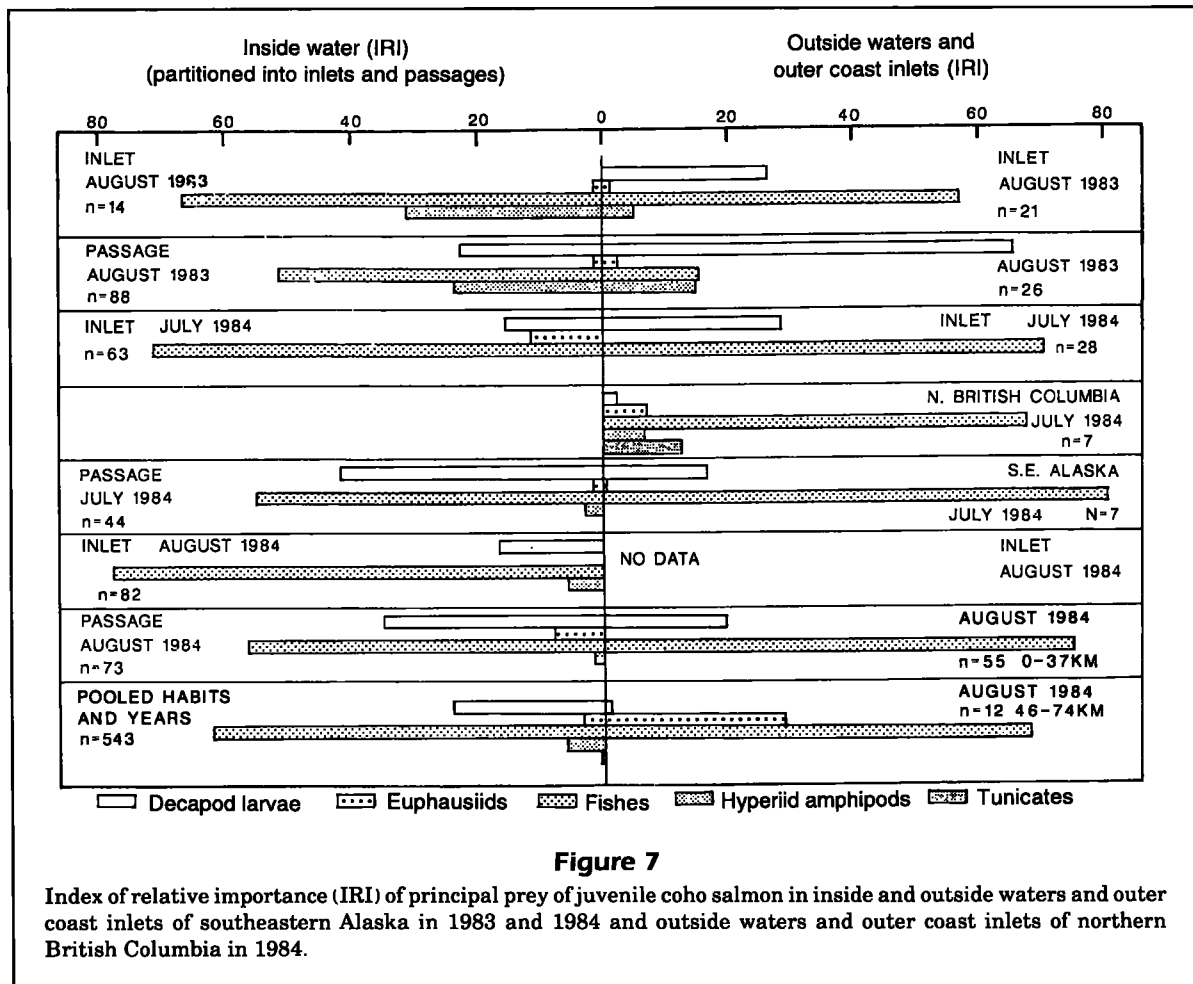
Salmon diet and the prey assemblages

Neuston samples from the outside waters of British Columbia and southeastern Alaska included 13 and 14 major taxa, respectively (Table 7). In British Columbia, decapod larvae made up 83% of the number of prey, hyperiid amphipods 12%, calanoid copepods 4%, and all other taxa <1%. Prey diversity of neuston samples was more even for southeastern Alaska than for British Columbia; half of the 14 taxa represented $\geq 2\%$ of the total abundance. In Alaska, calanoid copepods were the most abundant organism (59% of the total), decapod larvae were second (21%), and gammarid amphipods were third (9%). The density of neustonic organisms was about five

times greater in samples from British Columbia than in those from southeastern Alaska.

In zooplankton samples, the number of individuals and dominant taxa differed with time and habitat (Table 7). Zooplankton abundance in outside waters was about twice that of inside waters of southeastern Alaska in July 1984. Calanoid copepods were the dominant organisms in the samples (90% of total abundance).

The PSI indicated little relationship between prey consumed by salmon and prey available in the environment (Table 8). Neuston samples were generally more similar to salmon diet than were zooplankton samples. Similarity for the neuston samples ranged from 0% to 37.8% and averaged from 9.1% for sockeye salmon to 16.7% for coho salmon (Table 8). The PSI values for the plankton samples ranged from 0.2% to 24.9% and averaged from 2.2% for chum salmon to 9.3% for sockeye salmon.



We examined patterns of prey selectivity by applying Strauss's linear index of food selection to the same sets of predator-prey samples that had been analyzed for similarity. Pink and sockeye salmon selected ($L > 0.10$) neustonic prey more often than planktonic prey, and neustonic hyperiid amphipods were the most frequently selected organism. Chum and coho salmon selected neustonic and planktonic prey in nearly equal frequencies (Table 9). All salmon species avoided ($L < -0.10$) neustonic decapod larvae. Selection patterns for planktonic prey varied more than for neustonic prey; however, salmon generally selected planktonic decapod larvae, hyperiid amphipods, euphausiids, and fishes and avoided the proportionately more abundant calanoid copepods.

Discussion

This study of the food habits of five sympatric species of Pacific salmon during their first summer in

the marine waters of southeastern Alaska and northern British Columbia is the first detailed study for this geographic area. Feeding patterns were dynamic, with shifts in the important prey categories between salmon species, years, and areas.

We analyzed the importance of two major prey categories, zooplankton and teleosts, and examined data for temporal and spatial shifts in feeding patterns among salmon species. First, in pooled samples (all periods and habitats), zooplankton were much more important in pink, chum, and sockeye salmon diets (60–70% IRI) than in coho and chinook salmon diets (36% and 24% IRI; Table 3). When the two years of data were analyzed separately, however, contrasting patterns emerged. In 1983 (August), pink, chum, and sockeye salmon were mostly planktivorous (83–97% IRI), and zooplankton IRI was over 50% even for coho salmon. In 1984 (July and August), the proportional number, weight, and FO of teleost prey increased in diets of all salmon species; however, zooplankton remained most important in the diets of pink,

chum, and sockeye salmon (56–65% IRI), teleosts were most important in coho salmon diets (68% IRI).

Spatial factors that influence both predator and prey, especially latitude and proximity to shore, may account for similarities or differences in principal prey (Andrievskaya, 1970; Brodeur and Percy, 1990). Most species of salmon are opportunistic and feed on a wide variety of prey (Beacham, 1986; Brodeur¹), but their diets are commonly composed of a few taxa readily available at a given time and location. The importance of zooplankton in the diets of juvenile pink, sockeye, and chum salmon in our study is similar to results reported in other studies from the eastern Gulf of Alaska (Manzer, 1969; Jaenicke et al.,

1984; Hartt and Dell, 1986), the Sea of Okhotsk (Andrievskaya, 1968, 1970), and other regions of the northeastern Pacific Ocean (Peterson et al., 1982; Brodeur, 1989; Brodeur and Percy, 1990). We found that hyperiid amphipods were especially important in pink and sockeye salmon diets, and less so in chum salmon diets. The principal hyperiid amphipod found in diets of these species in the northeastern Pacific Ocean, including our study, was *Themisto pacifica*. In the more southern latitudes of coastal Washington and Oregon, another hyperiid amphipod (*Hyperoche medusarum*) is an important component in chum, coho, chinook, and sockeye salmon diets (Brodeur and Percy, 1990). In that area, however, euphausiids are more important in juvenile chum diets and, to a lesser extent in juvenile coho and chinook salmon diets, than are hyperiid amphipods (Peterson et al., 1982; Brodeur and Percy, 1990). Similarly, we found that euphausiids occurred less frequently and were less important in diets of all juvenile salmon located off southeastern Alaska, a downwelling region, compared to diets of salmon from southern British Columbia to Oregon, where upwelling is more prevalent (Ware and McFarlane, 1989).

Although our study showed that chum salmon are primarily planktivorous, like pink and sockeye salmon, we observed another difference in their most important prey. Tunicates (larvacea and salps) were important only in the diets of chum salmon. The IRI for tunicates, especially the larvacean *Oikopleura dioica*, was greater than for any other taxon in chum salmon diets (30.1%). Tunicates were most prevalent in samples from outer coast inlets and outside waters (0–37 km). This finding is not unusual. *Oikopleura* was the dominant prey item in two other studies of the diet of juvenile chum salmon from northern British Columbia: 62% FO in fish 32–106 mm FL from Chatham Sound (Manzer, 1969) and 70–76% FO in fish 105–158 mm FL from Hecate Strait (Healey, 1991).

In addition to interspecific differences in the most important prey, shifts in diet differed among the four salmon species both spatially and temporally. We observed spatial differences in July 1984, when sampling included waters of northern British Columbia, and in August 1984, when sampling was extended to 76 km offshore. Pink, chum, and sockeye salmon consumed fish prey about twice as often offshore as they did inshore, and more often in British Columbia than in Alaska. The more piscivorous coho salmon, however, consumed fish just as frequently inshore as offshore and just as frequently in marine waters of Alaska and British Columbia. Diet varied by season and distance offshore for the highly similar pink,

Table 4

Chi-square (χ^2) values for variation in frequency of occurrence of principal prey in four species of juvenile salmon. Comparisons were made between years (August 1983 and August 1984), months (July 1984 and August 1984), area (northern British Columbia and southeastern Alaska), and distance offshore (0–37km vs. 46–76km). No asterisk indicates $P > 0.05$. * = $P \leq 0.05$; ** = $P \leq 0.01$; and *** = $P \leq 0.001$.

Taxon	χ^2			
	Between years	Between months	Between areas	Between inshore and offshore
Pink salmon				
Calanoids	35.29***	0.07	2.47	0.35
Decapods	18.41***	0.07	1.82	13.04***
Euphausiids	11.35***	2.90	17.13***	3.86*
Hyperiiids	2.34	0.62	1.18	8.60***
Tunicates	7.13**	19.48***	6.08*	13.83***
Teleosts	6.39*	0.00	7.33**	47.72***
Chum salmon				
Calanoids	8.62***	0.25	6.08*	0.37
Decapods	4.02*	6.63*	2.04	5.94*
Euphausiids	9.06***	1.74	5.66*	5.15*
Hyperiiids	4.93*	0.01	0.12	15.30***
Tunicates	3.78	1.77	3.43	1.36
Teleosts	3.53	0.53	6.94**	26.46***
Sockeye salmon				
Calanoids	6.84**	3.73	3.72	0.08
Decapods	14.77***	26.12***	1.74	1.36
Euphausiids	19.47***	13.21***	14.81***	0.68
Hyperiiids	73.17***	57.10***	0.34	0.04
Tunicates	0.72	9.77***	5.45*	4.51*
Teleosts	11.05***	0.09	13.42***	12.69***
Coho salmon				
Calanoids	9.26***	4.35*	—	—
Decapods	14.96***	20.50***	0.00	1.46
Euphausiids	0.80	0.07	7.20**	3.98*
Hyperiiids	48.46***	0.11	3.86*	—
Tunicates	0.86	7.00**	0.33	—
Teleosts	5.77*	6.90**	1.84	0.59

Table 5

Diet overlap values (\hat{C}_i , Morisita's index for prey numbers; Horn, 1966) for inside and outside waters of British Columbia (BC) and Alaska by sampling period and pooled over time. Nearshore = 0–37 km; offshore = >37 km. An asterisk indicates a significant value.

Comparison	Diet overlap (\hat{C}_i)					Pooled over time
	Aug 1983	July 1984		August 1984		
		BC	Alaska	Nearshore	Offshore	
Inside inlets						
Pink-chum	0.55		0.87*	0.56		0.66*
Pink-coho	0.89*		0.04	0.29		0.41
Pink-sockeye	—		0.21	0.15		0.37
Chum-coho	0.47		0.11	0.14		0.24
Chum-sockeye	—		0.25	0.85*		0.51
Coho-sockeye	—		0.64*	0.01		0.55
Inside passages						
Pink-chum	0.94*		—	0.91*		0.91*
Pink-coho	0.54		0.11	0.09		0.25
Pink-sockeye	0.85*		0.49	—		0.58
Chum-coho	0.45		—	0.20		0.25
Chum-sockeye	0.74*		—	—		0.73*
Coho-sockeye	0.65*		0.46	—		0.49
Outside waters						
Pink-chum	—	0.44	0.82*	1.00*	0.85*	0.67*
Pink-coho	0.26	0.24	0.10	0.12	0.11	0.20
Pink-sockeye	0.77*	0.85*	0.97*	0.67*	0.79*	0.83*
Chum-coho	—	0.96*	0.10	0.10	0.09	0.32
Chum-sockeye	—	0.39	0.82*	0.53	0.97*	0.68*
Coho-sockeye	0.16	0.20	0.17	0.13	0.09	0.17
All habitats						
Pink-chum	0.95*		0.80*	0.88*		0.91*
Pink-coho	0.43		0.21	0.18		0.38
Pink-sockeye	0.72*		0.79*	0.99*		0.93*
Chum-coho	0.31		0.15	0.25		0.24
Chum-sockeye	0.58		0.73*	0.85*		0.73*
Coho-sockeye	0.62*		0.37	0.18		0.49

chum, and sockeye salmon in the Sea of Okhotsk and the Bering Sea (Andrievskaya, 1968). In our study, temporal patterns based on seasonal (monthly) differences in the FO of fish prey were rare; the diets of pink, chum, or sockeye salmon included fish as frequently in July 1984 (when transects extended only to 37 km) as in August 1984. However, interannual differences were observed: all species, except chum salmon, ate fish more frequently in August 1984 than in August 1983. These observations suggest that increased frequency of fish prey in salmon diets is related more to annual variations in teleost prey abundance than to distance offshore.

Juvenile fishes are often identified as important prey for juvenile salmon, although seldom to the extent that we observed in 1984 in northern southeastern Alaska. Comparison of our results with other studies of juvenile salmon diet in Alaska suggests

that, although pink, chum, and sockeye salmon feed principally on planktonic taxa, they readily switch to teleost prey when available. For example, crustaceans were the principal prey of pink, chum, and sockeye salmon in the outside waters of southeastern Alaska in 1982, whereas fish were the principal prey of coho salmon (Jaenicke et al., 1984). In our study in southeastern Alaska in 1983, prey fish made up only half as much biomass as that observed in juvenile sockeye salmon stomachs collected from the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986); in 1984, however, we recorded substantially higher teleost prey biomass than that observed by Hartt and Dell (Table 10). Although we found that sockeye salmon diet varied more than that of the other species, increases in the FO of predation on teleosts were consistent among pink, chum, and sockeye salmon.

Some of the interspecific differences in the utilization of fish prey may also be attributed to differences in predator size. The mean size of juvenile coho and chinook salmon was greater than that of pink, chum, and sockeye salmon. Although the importance of size-related variability in prey consumption of juvenile salmon is recognized (e.g. Brodeur, 1991), we considered that a detailed analysis by predator size was beyond the scope of this study.

Increased fish prey in the diets of juvenile salmon in 1984 may reflect higher abundances of larval and juvenile stages of certain prey species compared with the previous year. Unfortunately, most fish prey species found in the salmon stomachs in our study could not be identified. However, we noted opposite trends in the CPUE for two potential teleost prey species from 1983 to 1984: the CPUE of juvenile walleye pollock in our seine catches increased 25-fold whereas that of juvenile herring declined 40-fold. In 1984, juvenile walleye pollock were important in the diet of adult coho salmon (Fisk³); the conditions that prolonged offshore feeding by adult coho salmon on these fish in 1984 may also have favored increased piscivory by juveniles.

An increase in available fish prey between years may also correlate with an increase in environmental temperature. The average SST in 1984 (\bar{x} = 14.5°C) was higher than in 1983 (\bar{x} = 13.7°C). Increased SST in northern waters may have beneficial effects on the early life history of fish preyed upon by juvenile salmon (Bailey and Incze, 1985). Temperatures in outside waters in 1984 followed a long-term warming trend related to the 1982–83 El Niño event. Temperature increased at depth as well as at the surface, and positive temperature anomalies persisted in northern waters beyond 1983 (Cannon et al., 1985; Royer, 1985). In coastal waters off Oregon and Washington, oceanographic conditions varied greatly owing to the 1982–83 El Niño event and affected prey species composition, but the proportion of fish biomass in juvenile salmon diets generally did not vary for the same months between years (Brodeur and Percy, 1990).

Changes in salmonid diet patterns may reflect density-dependent species interactions. Other workers have noted such changes with respect to an increase in the density of pink salmon, typically the most abundant species: 1) the diet of other salmonids became more diverse, particularly in chum salmon; and 2) diet overlap among pink, chum, and sockeye salmon decreased (Birman, 1969; Andrievskaya,

Table 6

Estimated mean fullness (0=empty, 6=distended), degree of digestion (1=fresh, 4=completely digested), and percentage of empty stomachs for pooled habitats and time periods for juvenile salmon collected in marine waters of south-eastern Alaska and northern British Columbia in 1983 and 1984; *n* = sample size.

Habitat	<i>n</i>	Stomach fullness (0–6)	Degree of digestion (1–4)	Empty stomachs (%)
Pink salmon				
Inside inlet	70	4.0	1.9	0
Inside passage	223	3.9	2.3	0.4
Outer coast inlet	68	3.5	2.7	1.5
Outside (0–37 km)	361	3.0	2.2	3.3
Outside (>37 km)	93	4.0	2.3	0
Chum salmon				
Inside inlet	56	4.2	2.3	0
Inside passage	125	4.7	2.4	0
Outer coast inlet	62	4.6	2.2	0
Outside (0–37 km)	169	2.6	2.7	5.3
Outside (>37 km)	41	3.3	2.4	0
Sockeye salmon				
Inside inlet	24	4.3	2.5	0
Inside passage	58	4.5	3.0	1.7
Outer coast inlet	0	—	—	—
Outside (0–37 km)	227	3.4	2.3	0.9
Outside (>37 km)	52	3.6	2.5	0
Coho salmon				
Inside inlet	159	4.2	2.3	1.3
Inside passage	205	4.4	2.3	0.5
Outer coast inlet	52	4.2	2.5	0
Outside (0–37 km)	115	4.0	2.4	0
Outside (>37 km)	12	4.3	3.0	0

1970; Tadokoro et al., 1996). In the Sea of Okhotsk, diet overlap was lower in the coastal zone, where salmon density was greatest (Andrievskaya, 1970). We did not observe such density effects. We found significant diet overlap even in the four cases out of five where density effects could have been demonstrated among these species (see Jaenicke and Celewycz, 1994). The exception, when chum salmon diet did not overlap significantly with either pink or sockeye salmon diets, occurred during July 1984 in the outside waters of British Columbia.

Density-dependent effects on diet may be reflected in a third dietary attribute, the amount of food consumed. In the eastern coastal zone of the Sea of Okhotsk, for example, 30% of juvenile pink salmon and 66% of juvenile chum salmon sampled with gill nets (time of day not presented) had empty stomachs, a condition not found offshore, where juvenile salmon density was lower (Andrievskaya, 1970). Feeding conditions appeared to be much better for

³ Fisk, G. 1985. Final report 1984 troll logbook program. Alaska Trollers Assoc., 130 Seward St., No. 213, Juneau, AK 99801, 41 p.

Table 7

Neuston and zooplankton organisms (number per 100 m³) from outside- and inside-water habitats in British Columbia (BC) and Alaska, collected in July 1984.

	Zooplankton				
	Neuston		Outside		
	Outside BC	Combined Alaska	BC	Alaska	Inside Alaska
Number of samples	20	16	3	9	5
Invertebrate eggs	—	—	343.00	1,449.78	304.20
Polychaeta	0.13	0.13	—	—	—
Gastropoda	—	—	—	—	—
<i>Limacina helicina</i>	—	—	124.67	243.67	62.80
Bivalvia	—	—	—	—	26.60
Cephalopoda	0.05	0.13	31.00	—	—
Cladocera	—	—	145.33	524.00	234.20
Calanoida	39.77	114.56	48,672.34	60,074.67	25,956.00
Harpacticoida	0.50	4.31	0	34.33	5.20
Cirripedia	1.90	0.75	187.00	3,203.44	543.40
Mysidacea	—	0.13	0	579.89	—
Gammarideia	0.92	18.17	0	2.22	—
Hyperideia	126.12	5.21	436.33	566.33	1,142.00
Euphausiacea	8.86	0.17	4,072.70	126.78	164.80
Decapoda	873.11	40.18	363.67	510.33	230.00
Insecta	0.21	0.21	—	—	3.00
Chaetognatha	0.34	5.63	249.33	171.67	42.20
Larvacea	0.15	5.00	62.33	262.78	204.00
Teleosts ¹	1.46	0.79	31.00	6.11	—

¹ Eggs, larvae, and juveniles combined.

salmon in our study (seined during the day); of 2,216 stomachs examined, only 32 (1.4%) were empty. Although we found few empty stomachs, we did find evidence of decreased feeding in the 0–37 km region of outside waters, which includes the region of peak catches of pink and chum salmon (Jaenicke and Celewycz, 1994); fullness was lower for all species, and empty stomachs were most common for pink and chum salmon collected in these outside waters.

Juvenile coho salmon diet rarely showed significant overlap with pink, chum, and sockeye salmon diets. Coho salmon differed in distribution and size from the other three species (Jaenicke and Celewycz, 1994) and were more piscivorous. Curves of cumulative number of taxa (Fig. 3) sloped more steeply for coho salmon than for the other species; this rapid rate of increase in prey types may reflect opportunistic feeding of juvenile coho salmon. Diets are even more diverse among coho salmon individuals than among pink salmon individuals, which consumed a similarly broad array of prey taxa. Less aggregation and lower densities (CPUE) than those for other salmon (Jaenicke and Celewycz, 1994) allow coho salmon to exploit fully all locations within a habitat type. The other three species tended to occur in fewer

Table 8

Mean percent similarity index (PSI) values indicating amount of overlap between prey fields and juvenile salmon diet. Stations where prey were collected were included in the analysis for a particular salmon species if at least five stomachs were collected at the station.

	Number of stations	Similarity values	
		Mean	Range
Neuston collection			
Pink	8	10.8	0–24.6
Chum	2	9.3	0–18.5
Sockeye	8	9.1	0–37.8
Coho	2	16.7	0–33.3
Zooplankton collection			
Pink	8	8.0	1.0–22.7
Chum	5	2.2	0.2–6.8
Sockeye	4	9.3	1.0–24.9
Coho	6	6.2	0.7–11.7

locations (although they were well represented within habitat types) and tended to be more highly aggregated, increasing the tendency toward more

Table 9

Prey selection frequencies (Strauss's linear index of food selection (L); Strauss 1979) in juvenile salmon diet for neuston and zooplankton collections, July and August 1984. A positive (pos.) value indicates that a prey was more abundant in the diet than in the environment at a level of ≥ 0.10 . A negative (neg.) value indicates that a prey was less abundant in the diet than in the environment at a level of ≤ 0.10 . A random (ran.) value indicates that a prey was about equally abundant in the diet and in the environment. Absent indicates that a prey item was absent from the diet and from the environment in a particular location. N = number of groups tested, where group size was 5 or more of a species.

Taxon	Prey selection frequency															
	Pink salmon				Chum salmon				Sockeye salmon				Coho salmon			
	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent	Pos.	Neg.	Ran.	Absent
Neuston																
Polychaetes	0	0	1	7	0	0	0	2	0	0	0	8	0	0	0	2
Pteropods	1	0	2	5	0	0	2	2	0	0	0	8	0	0	0	2
Squid	0	1	0	7	0	0	0	2	0	0	0	8	0	0	0	2
Calanoid copepods	1	1	4	2	0	0	0	2	4	2	1	1	0	0	0	2
Barnacle larvae	0	0	0	8	0	0	0	2	0	1	0	7	0	0	0	2
Gammarid amphipods	0	2	2	4	0	1	0	1	0	1	1	6	0	1	0	1
Hyperiid amphipods	5	1	1	1	1	0	0	1	6	2	0	0	0	1	0	1
Euphausiids	4	1	1	2	0	0	1	1	3	1	1	3	0	0	1	1
Decapod larvae	2	4	1	1	0	2	0	0	2	3	1	2	1	1	0	0
Insects	0	0	1	7	0	0	0	2	0	0	0	8	0	0	0	2
Chaetognaths	0	0	2	6	1	0	0	2	0	0	1	7	0	0	0	2
Salps	0	0	0	8	0	0	0	2	0	0	0	8	0	0	1	1
Larvaceans	1	0	3	4	1	0	0	1	1	0	0	7	1	0	1	0
Teleosts	1	0	5	2	0	0	1	1	0	0	5	3	1	0	0	1
Percent selection	13.5	9.0	20.7	57.4	7.2	10.7	14.3	74.8	14.4	9.0	9.0	67.9	10.8	10.8	10.8	67.7
Plankton																
Cnidaria	0	0	3	5	0	0	2	3	0	0	2	2	0	0	1	5
Polychaetes	0	0	0	8	0	0	1	4	0	0	0	4	0	0	1	5
Pteropods	1	0	1	6	0	0	0	5	0	0	1	3	0	0	1	5
Bivalve larvae	0	0	0	8	0	0	0	5	0	0	0	4	0	1	1	4
Squid	0	0	0	8	0	0	0	5	0	0	1	3	0	0	0	6
Invertebrate eggs	0	2	1	5	0	1	0	4	0	1	0	3	0	0	1	5
Calanoid copepods	0	7	0	1	0	4	0	1	0	4	0	0	0	6	0	0
Barnacle larvae	0	0	2	6	0	0	1	4	0	1	1	2	0	1	1	4
Mysids	0	0	0	8	0	0	0	5	0	0	0	4	0	0	0	6
Hyperiid amphipods	2	0	2	4	2	0	1	2	2	0	1	1	1	0	4	1
Euphausiids	2	0	2	4	1	0	1	3	1	0	1	2	2	0	3	1
Decapod larvae	4	0	1	3	1	0	2	2	2	0	1	1	5	0	1	0
Insects	0	0	0	8	0	0	0	5	0	0	0	4	0	0	2	4
Cladocera	0	0	0	8	0	0	0	5	0	0	1	3	0	0	2	4
Chaetognaths	0	0	2	6	0	0	0	5	0	0	2	2	0	0	1	5
Salps	0	0	1	7	0	0	1	4	0	0	0	4	0	0	1	5
Larvaceans	2	0	1	5	2	0	1	2	0	0	2	2	1	0	3	2
Teleosts	1	0	2	5	1	0	1	3	1	0	3	0	3	0	2	1
Percent selection	8.4	6.3	12.6	73.5	7.7	5.5	12.1	73.7	8.4	8.4	21.0	61.6	11.1	7.4	23.1	58.2

similar diets. Many seine sets caught only coho salmon, whereas catches of the more highly aggregated species often also contained coho salmon. In laboratory experiments, coho salmon smolts in seawater demonstrated agonistic behavior which, if occurring in the wild, would maintain discrete feeding territories and a dispersed population (Paszowski and Olla, 1985).

Differences in diet, distribution, and size indicate that juvenile coho salmon have a distinct feeding ecology in comparison with these other, more planktivorous, juvenile salmon co-occurring in the southern Gulf of Alaska. In both our study and that of Brodeur and Pearcy (1990), fish were more important in the diets of juvenile coho salmon than in other species. During the second year of our study—when

Table 10

Principal prey of juvenile sockeye salmon in southeastern Alaska and northern British Columbia in 1983 and 1984 and in the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986). Values are percent biomass of total diet. The number of fish sampled is shown in parentheses, followed by fork length ranges (mm).

Prey	Pooled 1967-68 (996)	Pooled 1983-84 (361)	August 1983 (55)	July 1984 (159)	August 1984 (147)
	130-180	100-300	130-249	100-209	110-300
Copepods	5.1	0.5	4.6	0.4	0.5
Decapod larvae	—	2.6	8.3	0.8	5.3
Euphausiids	42.0	4.3	39.0	3.4	3.8
Amphipods	1.6	3.7	30.7	2.0	5.1
Pteropods	6.2	—	—	—	—
Larval fish	30.8	87.2	16.7	92.0	83.1

teleost prey increased in all diets—pink, chum, and sockeye salmon readily switched from small zooplankton to larger teleost prey in response to an apparent increase of available larval fish prey. The ability of salmon species to maintain plasticity in their diets may be an adaptation to changing ocean conditions—one that may improve marine survival.

On the basis of our comparisons between the prey composition of juvenile salmonids and the taxa found in neuston and plankton tows, we conclude that these juveniles are selecting a limited subset of available prey. Although other factors besides feeding preferences (e.g. prey patchiness, gear selectivity, differential digestion rates of prey) could lead to low selectivity values, certain taxa do appear to be consumed in high proportions in relation to their abundance. Our results suggest that juvenile salmon are visual predators and select prey on the basis of prey size and visibility and not on local abundance. For example, relatively rare hyperiid amphipods were selected by most salmon, whereas slightly smaller but much more numerous copepods were ignored. As observed by Peterson et al. (1982), this prey selection may be due to the heavy pigmentation and unusual swimming motion of hyperiids in contrast to the light pigmentation and fast swimming motion of copepods.

Although the diets of both chum and coho salmon appear to be more similar to the neuston than the zooplankton catches, a reliance on neustonic fauna, as suggested by Brodeur (1989) for coho salmon off Washington and Oregon, is not conclusively demonstrated because of the small number of comparisons that we were able to make. More detailed field and laboratory studies are required to determine whether

juvenile salmon show a reliance on certain prey or an inability to switch to alternate prey when preferred prey resources are depleted. Under these conditions, the availability of the right kinds of prey may have more important implications for the survival of juvenile salmon in coastal waters than the overall production of prey.

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Literature cited

- Andrievskaya, L. D.**
1968. Feeding of Pacific salmon fry in the sea. *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.* (TINRO) 64:73-80. [In Russ.; Engl. transl. 1970, Fish. Res. Board Can. Transl. Ser. 1423, 16 p.]
- 1970.** Feeding of Pacific salmon juveniles in the Sea of Okhotsk. *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.* (TINRO) 78:105-115. [In Russ.; Engl. transl. 1973, Fish. Res. Board Can. Transl. Ser. 2441, 20 p.]
- Bailey, K. M., and L. S. Incze.**
1985. El Niño and the early life history and recruitment of fishes in temperate marine waters. In W. S. Wooster and D. L. Fluharty (eds.), *El Niño North: Niño effects in the eastern subarctic Pacific Ocean*, p.143-165. Washington Sea Grant WSG-WO-85-30, Univ. Washington, Seattle, WA, 312 p.
- Beacham, T. D.**
1986. Type, quantity, and size of food of Pacific salmon (*Oncorhynchus*) in the Strait of Juan de Fuca, British Columbia. *Fish. Bull.* 84:77-89.
- Beamish, R. J., and D. R. Bouillon.**
1993. Pacific salmon production trends in relation to climate. *Can. J. Fish. Aquat. Sci.* 50:1002-1016.
- Birman, I. B.**
1969. Distribution and growth of young Pacific salmon of the genus *Oncorhynchus* in the sea. *Probl. Ichthyol.* 9:651-666.
- Brodeur, R. D.**
1989. Neustonic feeding by juvenile salmonids in coastal waters of the Northeast Pacific. *Can. J. Zool.* 67:1995-2007.
- 1991.** Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. *Env. Biol. Fishes* 30:303-315.

- Brodeur, R. D., and W. G. Pearcy.**
1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. *Fish. Bull.* 88:617-636.
- Brodeur, R. D., and D. M. Ware.**
1995. Interdecadal variability in distribution and catch rates of epipelagic nekton in the Northeast Pacific Ocean. In R. J. Beamish (ed.), *Climate change and northern fish populations*. *Can. Spec. Publ. Fish. Aquat. Sci.* 121, p. 329-356.
- Cannon, G. A., R. K. Reed, and P. E. Pullen.**
1985. Comparison of El Niño events off the Pacific Northwest. In W. S. Wooster and D. L. Fluharty (eds.), *El Niño North: Niño effects in the eastern subarctic Pacific Ocean*, p. 75-84. Washington Sea Grant WSG-WO-85-3, Univ. Washington, Seattle, 312 p.
- Groot, C., and L. Margolis.**
1991. Pacific salmon life histories. Univ. British Columbia, Vancouver, 564 p.
- Hartt, A. C., and M. B. Dell.**
1986. Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. *Int. North Pac. Fish. Comm. Bull.* 46, 105 p.
- Healey, M. C.**
1991. Diets and feeding rates of juvenile pink, chum, and sockeye salmon in Hecate Strait, British Columbia. *Trans. Am. Fish. Soc.* 120:303-318.
- Helle, J. H.**
1989. Relation between size-at-maturity and survival of progeny in chum salmon, *Oncorhynchus keta* (Walbaum). *J. Fish Biol.* 35(suppl. A):99-107.
- Helle, J. H., and M. S. Hoffman.**
1995. Size decline and older age at maturity of two chum salmon (*Oncorhynchus keta*) stocks in western North America, 1972-92. In R. J. Beamish (ed.), *Climate change and northern fish populations*. *Can. Spec. Publ. Fish. Aquat. Sci.* 121, p. 245-260.
- Horn, H. S.**
1966. Measurement of "overlap" in comparative ecological studies. *Am. Naturalist* 100:419-424.
- Hurtubia, J.**
1973. Trophic diversity measurement in sympatric predatory species. *Ecology* 54:885-890.
- Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and K. Nagasawa.**
1993. Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in the North Pacific Ocean and possible causes. *Can. J. Fish. Aquat. Sci.* 50:290-295.
- Jaenicke, H. W., and A. G. Celewycz.**
1994. Marine distribution and size of juvenile Pacific salmon in Southeast Alaska and northern British Columbia. *Fish Bull.* 92:79-90.
- Jaenicke, H. W., R. D. Brodeur, and T. Fujii.**
1984. Exploratory gillnetting from the *Oshoro-maru* for juvenile salmonids off southeastern Alaska, 24-25 July 1982. *Bull. Fac. Fish. Hokkaido Univ.* 35(3):154-160.
- Kaeriyama, M.**
1989. Aspects of salmon ranching in Japan. *Physiol. Ecol. Japan, spec. vol.* 1:625-638.
- Manzer, J. I.**
1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. *J. Fish. Res. Board Can.* 26:2219-2223.
- McNeil, W. J., and D. C. Himsworth (eds.)**
1980. Salmonid ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis, OR, 331 p.
- Paszkowski, C. A., and B. L. Olla.**
1985. Social interactions of coho salmon (*Oncorhynchus kisutch*) smolts in seawater. *Can. J. Zool.* 63:2401-2407.
- Pearcy, W. G.**
1992. Ocean ecology of North Pacific salmonids. Univ. Washington Sea Grant, Seattle, WA, 179 p.
- Peterson, W. T., R. D. Brodeur, and W. G. Pearcy.**
1982. Food habits of juvenile salmon in the Oregon coastal zone, June 1979. *Fish. Bull.* 80:841-851.
- Pinkas, L., M. S. Oliphant, and I. L. K. Iverson.**
1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *Calif. Dep. Fish Game, Fish. Bull.* 152, 105 p.
- Royer, T. C.**
1985. Coastal temperature and salinity anomalies in the northern Gulf of Alaska, 1970-84. In W. S. Wooster and D. L. Fluharty (eds.), *El Niño North: Niño effects in the eastern subarctic Pacific Ocean*, p. 107-115. Washington Sea Grant WSG-WO-85-3, Univ. Washington, Seattle, WA, 312 p.
- Strauss, R. E.**
1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans. Am. Fish. Soc.* 108:344-352.
- Tadokoro, K., Y. Ishida, N. D. Davis, S. Ueyanagi, and T. Sugimoto.**
1996. Change in chum salmon (*Oncorhynchus keta*) stomach contents associated with fluctuation of pink salmon (*O. gorbuscha*) abundance in the central subarctic Pacific and Bering Sea. *Fish. Oceanog.* 5(2):89-99.
- Ware, D. M., and G. A. McFarlane.**
1989. Fisheries production domains in the Northeast Pacific Ocean. In R. J. Beamish and G. A. McFarlane (eds.), *Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models*, p. 359-379. *Can. Spec. Publ. Fish. Aquat. Sci.* 108.
- Wertheimer, A. C.**
1997. Status of Alaska salmon. In D. J. Stouder, P. A. Bisson, and R. J. Naiman (eds.), *Pacific salmon and their ecosystems*, p. 179-197. Chapman and Hall, New York, NY, 685 p.
- Whittaker, R. H.**
1975. *Communities and ecosystems*, 2nd ed. MacMillan Co., New York, NY, 385 p.