Abstract. – Feeding habits of juvenile coho *Oncorhynchus kisutch*, chinook *O. tshawytscha*, chum *O. keta*, and sockeye *O. nerka* salmon were examined from collections taken off the Oregon–Washington coast during the summers of 1980–85. The major prey of both coho and chinook salmon juveniles were larval and juvenile fishes, although a substantial proportion of the diet of coho salmon consisted of invertebrates such as euphausiids, decapod larvae, and hyperiid amphipods. Juvenile chum and sockeye salmon had a more varied diet consisting generally of smaller prey, such as juvenile euphausiids, copepods, amphipods, and chaetognaths. Diet overlap was highest between coho and chinook salmon. Both dietary overlap and diversity varied substantially among cruises and individual collections.

Pronounced seasonal and interannual variations occurred in the utilization of the major prey taxa by coho and chinook salmon which may have been related to highly variable oceanographic conditions prevailing during this period. Areal (latitudinal and cross-shelf) variations were of lesser importance in the diets of juvenile coho and chinook salmon.

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Trophic Relations of Juvenile Pacific Salmon off the Oregon and Washington Coast

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Until recently, much of the interannual variability in the survival of Pacific salmon *Oncorhynchus* spp. was believed to be a result of conditions occurring in freshwater. It was surmised that by releasing high and relatively constant numbers of hatchery smolts in freshwater, much of the interannual variation in salmon production could be circumvented. Contrary to this assumption, a number of recent studies have found that a substantial portion of the total natural mortality for most salmon species may occur during estuarine and early marine residence (Parker 1968, 1971; Mathews and Buckley 1976; Bax 1983; Furnell and Brett 1986; Fisher and Pearcy 1988). For coho salmon *O. kisutch* originating from Oregon and Washington rivers, peak mortality appears to happen very early in the ocean, perhaps within the first month, and year-class size appears to be well established by the end of the first summer in the ocean (Pearcy 1988).

We still do not know the exact cause of this early ocean mortality. Annual variability in ocean survival of Oregon–Washington salmon stocks appears to be quite large. Both depensatory environmental factors, such as upwelling (Gunsolus 1978, Nickelson 1986), and compensatory biotic interactions such as competition or predation (Peterman 1982, Peterman and Routledge 1983, McGie 1984) have been implicated in the early ocean mortality of juvenile salmon. In either situation, early ocean feeding may be important, and perhaps critical, to growth and survival of salmonids.

Knowledge of the feeding habits and diet variability of juvenile salmon in the coastal ecosystem off Washington and Oregon is incomplete. Peterson et al. (1982) described the diets of juvenile coho, chinook *O. tshawytscha*, and chum *O. keta* salmon for one month (June 1979) and three different geographical areas off southern Washington and Oregon. Emmett et al. (1986) examined seasonal variations in juvenile coho and chinook salmon feeding habits from three time-periods during 1980, but did not examine geographic variations in any detail. There were substantial within and between-study differences in the food composition of these salmonids, although the relative importance of the geographical and temporal components of the variability could not be assessed because of the different sampling designs of the two studies.

This paper describes the diet composition and feeding relationships of juvenile coho, chinook, chum, and sockeye (*O. nerka*) salmon collected from coastal waters off Washington and Oregon during a series of summer purse-seine collections made from 1980 to 1985. Oceanographic conditions and biological productivity were highly variable during this period, both seasonally and interannually (Fisher and Pearcy 1985, Brodeur and Pearcy 1986), and thus provided a fortuitous situation in which to examine the effects of environmental variability on juvenile salmon feeding habits. In addition to examining the interannual variation in feeding, the broad seasonal and geographic coverage of the sampling permitted more detailed intra-annual and areal resolution than was previously possible. Particular detail will be provided for coho and chinook salmon juveniles, which were the dominant salmonids caught (Pearcy 1984, Pearcy and Fisher In press). Although the importance of other potential sources of variability in the diet, such as those attributable to the time of day and predator size, is recognized, these additional factors are discussed in detail elsewhere (Brodeur and Pearcy 1987, Brodeur In press).

Methods

Collection of stomachs

Juvenile salmon were collected with small-mesh (32 mm stretched), large volume (up to 1 million m^3) herring purse seines (Pearcy and Fisher 1988). Sampling was conducted in known areas of salmon concentration in 1980; in following years, predesignated stations were sampled along parallel transect lines spaced approximately 37 km apart (Fig. 1). Along each transect, stations were located every 9.3 km (5 miles) beginning onshore at the 37-m (20 fm) isobath and continuing out to 56 km from the coast or until no juvenile salmon were caught. Data from a total of 15 cruises have been included in this study, with at least one cruise taking place during every month from May through September (Table 1). June was the most intensely sampled month and was sampled during each of the 6 years of the study.

Most collections were made during daylight or twilight, although several complete diel series were made (Brodeur and Pearcy 1987). Circular, quantitative haul sets were made at most stations, although a small proportion of the fish used in this study were collected from sets which were held open for up to 45 minutes or from non-quantitative sets (Pearcy and Fisher 1988). After pursing the net, the catch was then concentrated in the bunt of the seine, and either dip-netted out from the seine or hauled onboard the stern of the sampling vessel. Total sampling time for most sets was approximately 20 minutes. Ancillary physical (temperature and salinity) and biological (chlorophyll *a* and some zooplankton) data were collected before or after the fish collections. A detailed listing of the station locations and many of the physical and biological measurements are given by Fisher and Pearcy (1985) and Brodeur and Pearcy (1986).

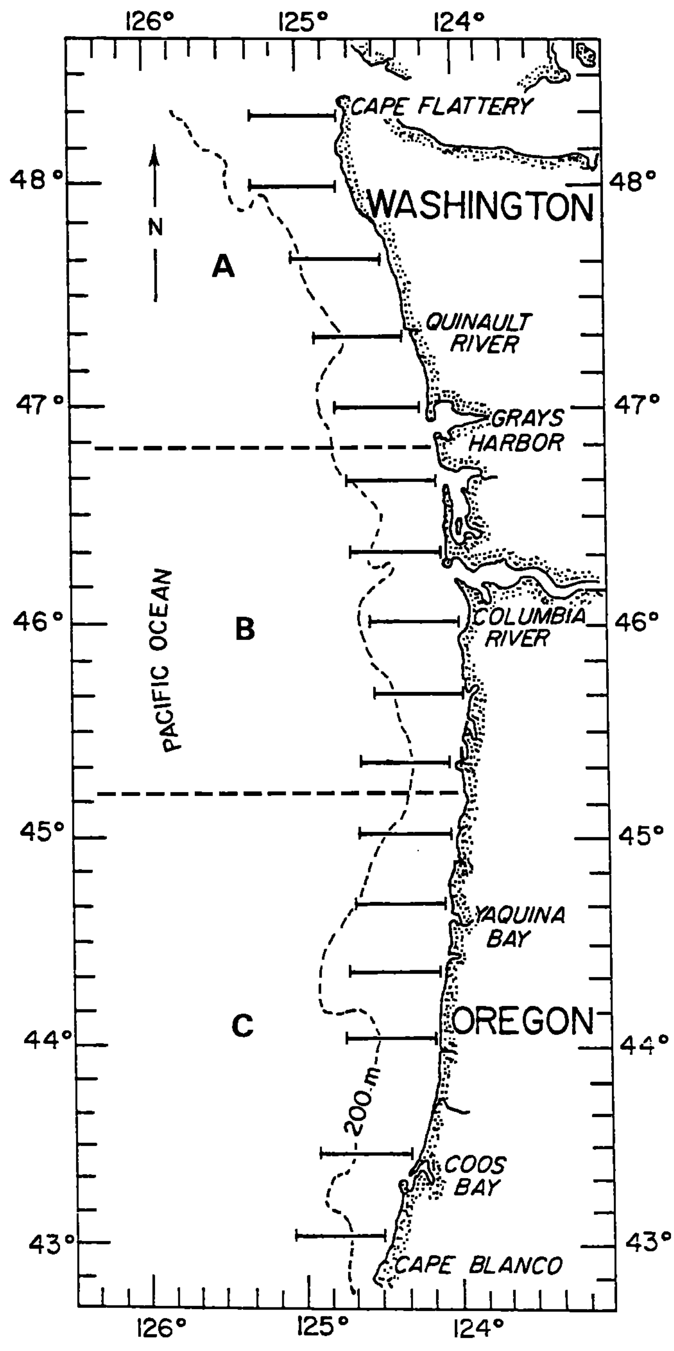

Figure 1
Location of sampling transects and geographic subareas defined in this study.

Table 1
Summary of sampling off Oregon and Washington by cruise from 1980 to 1985. Number of sets includes only quantitative, round hauls taken within 56 km of the coast.

Cruise no.	Year	Dates of cruise	Latitudinal range sampled (North latitude)	Number of sets
1	1980	June 20–28	46°20′–44°30′	33
2	1981	May 16–25	46°35′–44°30′	63
3	1981	June 9–19	46°35′–43°11′	67
4	1981	July 9–19	46°35′–44°25′	71
5	1981	August 8–19	46°35′–43°11′	66
6	1982	May 19–June 2	48°20′–44°00′	62
7	1982	June 7–22	47°20′–44°20′	56
8	1982	Sept. 4–14	47°20′–44°20′	40
9	1983	May 16–27	48°20′–44°20′	57
10	1983	June 9–27	48°20′–43°00′	58
11	1983	Sept. 15–24	48°20′–43°28′	52
12	1984	June 6–20	48°20′–43°28′	66
13	1984	July 19–30	48°00′–44°00′	40
14	1984	Sept. 1–15	48°20′–44°00′	63
15	1985	June 10–25	48°00′–43°27′	78
			Total	865

Once aboard, the juvenile salmon were quickly separated from the rest of the catch and anaesthetized in MS-222 to prevent regurgitation during handling. Each fish was tentatively identified, measured to the nearest mm (fork length), individually labeled, and either preserved whole in formalin after slitting the body cavity (1980 and part of 1981) or frozen whole in a −20°C freezer.

In the laboratory ashore, species identifications were verified and individual wet weights were recorded to the nearest 0.1 g. Stomachs were then removed from a random subsample of up to 10 individuals per species for each collection, with the stipulation that the entire size range of each species represented in the sample be included. Stomachs were individually preserved in a 10% formalin solution and then transferred to a 70% ethanol solution prior to examination. Subyearling and yearling juveniles of each species in their first year in the ocean were distinguished from adult fish using scale analysis (Fisher and Pearcy 1988).

Stomach analysis

Stomachs were opened and the relative fullness was subjectively assessed on a scale from 0 (empty) to 5 (fully distended). The entire stomach contents were blotted on absorbent paper to remove excess moisture and weighed to the nearest 1 mg. The contents were identified under a dissecting microscope to the lowest possible taxonomic level and life-history stage. During this analysis, each prey taxon was assigned a digestion code ranging from 0 (well digested) to 4 (fresh), and a digestion level for the entire stomach was derived from these codes based on the relative proportion by weight of each taxon. Each prey taxon was then enumerated, blotted to remove excess moisture, and weighed to the nearest 1 mg.

Statistical analyses

Three measures were used to determine the importance of each prey taxon to a particular predator: the percent frequency of occurrence in non-empty stomachs (F), the percent of total number of prey organisms (N), and the percent of total weight of prey organisms (W). These measures were combined into a single number, the Index of Relative Importance (IRI = F (N + W)), modified from that described by Pinkas et al. (1971) using weight instead of volume, so that comparisons can easily be made between the relative prey composition of different collections or species. Prey items that were digested or taxa difficult to count, such as gelatinous organisms, were not assigned IRI values. The IRI values were then converted to percent of total IRI for each predator species.

Niche breadth, expressed as the scope of utilization of food resources by each predator species, was calculated using the Shannon-Weaver formula:

$$H'_i = -\sum_{j=1}^{n} P_{ij} (\log_2 P_{ij})$$

where P_{ij} = the proportion by weight of a prey item j in predator i (Petraitis 1979). This index is influenced by both the number of species in the stomachs and the evenness with which they are distributed among the stomachs, and attains a maximum value (H'_{max}) of $\log_2$ (number of prey taxa). The ratio of H' to H'_{max} provides a measure of the evenness with which the resources are distributed among the predators (Pielou 1977).

Diet overlap was calculated among all species for the entire data set and between coho and chinook by cruise or collection where at least 10 stomachs of each species were examined. Schoener's Percent Similarity Index (PSI) was used since it was found to have the most favorable properties within the range of normal overlap values in the absence of prey availability data (Linton et al. 1981, Wallace 1981) where:

$$PSI = [1.0 - 0.5 (\sum | P_{ij} - P_{hj} |)] \times 100$$

where P_{ij} is the proportion by weight of food category

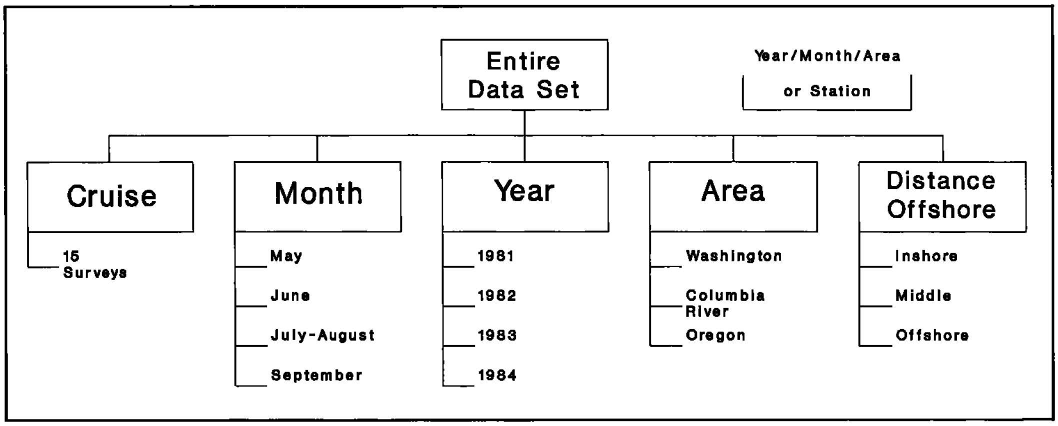

Figure 2
Hierarchy of data groupings used in the analysis of dietary variations in juvenile Pacific salmon.

j in the diet of species i, and P_{hj} is the proportion by weight of food category j in the diet of species h. This index ranges from 0 when two predators have no prey in common to 100 when they have identical diets. Overlap values greater than 60 are generally considered significant. Food availability was considered to be the same for all predators in any one comparison.

The detailed stomach data were then truncated to major taxonomic categories so that general trends in feeding by month, year, and area could be elucidated. Stomach samples of each salmon species were grouped into smaller subsets in a number of different ways to examine diet variability (Fig. 2). The diets of coho and chinook salmon were first examined by cruise so that temporal variability between cruises could be assessed. Data were then grouped by month into four time-periods: May (three cruises), June (six cruises), July–August (three cruises), and September (three cruises). Seasonal changes in diets were then analyzed for these time-periods, regardless of the year or area of collection. Similarly, diets were analyzed by year of collection for those years (1981–84) when multiple cruises exist. North-south geographic variations were examined for each of three subareas within the total sampling area. The collections were stratified latitudinally (Fig. 1) into three areas: (A) north of 46°40′N, (B) between 46°40′N and 45°20′N, and (C) south of 45°20′N (Brodeur et al. 1987a). Food habits were examined for each of these areas for all months and years combined. Finally, diets were examined within each year/month/area subset or by collection so that smaller-scale variations in the food and dietary overlap could be assessed.

Another potential source of geographic variability was that associated with inshore-offshore variations in prey availability and abundance. This source of variation was examined for several cruises where a large number of collections of coho or chinook salmon were obtained far offshore. For these cruises, collections were divided into inner shelf (<18 km from shore), middle shelf (18–37 km), and outer shelf (>37 km) stations. Diets of chum and sockeye salmon were also examined for variation with respect to the different factors when sample sizes were adequate.

The relative importance of the interannual, seasonal, and geographic variations seen in the diets of coho and chinook juveniles was tested by comparing the presence and absence of a particular major prey category using a variance test of binominally distributed data (Snedecor and Cochran 1967) for each factor individually irrespective of the others. When a value exceeded the tabulated 0.05 chi-square percentage, the null hypothesis that the diets were similar was rejected.

Results

Coho salmon

General food habits Juvenile coho salmon had a relatively diverse diet with many different prey categories represented in the stomachs examined for all years combined (Appendix Table 1). A high percentage (95.2%) of the stomachs contained food, and the overall stomach fullness ($\bar{x}$ 3.0) and digestion ($\bar{x}$ 2.3) codes were high indicating that many of the juvenile coho had fed prior to capture.

The primary food groups consumed by juvenile coho salmon were fishes, decapod larvae, amphipods, euphausiids, pteropods, and copepods (Appendix Table 1). Larval and juvenile fishes were the most important prey making up 72% of the total weight and 60% of the total IRI. Rockfishes *Sebastes* spp., northern anchovies *Engraulis mordax*, and Pacific sand lance *Ammodytes hexapterus* were the dominant fish taxa. Although other fish families were represented in the diet, notably the Osmeridae, Cottidae, Hexagrammidae, and Pleuronectidae, each of these families made up less than 1% of the total diet by percent IRI.

Table 2

Food habits by percent weight of major food categories for coho salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	82.8	75.6	73.3	17.6	65.1	75.6	75.6	83.1	73.2	82.7	81.9	83.6	26.1	61.0	82.1
Euphausiids	4.4	2.0	11.0	22.2	31.7	16.0	13.3	2.9	7.3	0.7	10.5	4.9	15.2	17.5	6.3
Decapods	3.5	8.4	11.9	3.5	0.3	6.9	4.2	0.6	12.8	15.6	0.1	10.9	13.2	5.6	6.3
Hyperiids	0.9	0.7	0.4	3.9	1.2	0.8	3.9	5.7	1.5	0.6	3.9	0.1	3.5	13.4	4.8
Pteropods	0.2	10.1	1.6	51.1	0.3	0.3	0.3	6.7	1.6	<0.1	2.1	—	0.1	0.5	<0.1
Copepods	<0.1	0.2	0.3	0.3	0.1	<0.1	<0.1	<0.1	1.3	0.1	<0.1	0.3	0.4	<0.1	<0.1
Insects	<0.1	—	<0.1	0.1	0.1	0.2	0.1	<0.1	0.3	<0.1	<0.1	<0.1	40.0	<0.1	0.1
Cephalopods	6.9	0.6	0.3	—	1.2	—	—	0.9	<0.1	—	1.3	—	0.4	1.0	—
Other*	1.1	0.4	0.8	0.8	<0.1	1.8	1.0	<0.1	0.2	<0.1	0.1	0.1	1.2	<0.1	0.4
Predator characteristics															
No. stomachs	77	245	139	115	94	57	124	144	112	125	102	81	75	61	101
No. empty	1	15	13	3	6	1	4	5	1	7	3	7	7	3	3
Mean length	167.9	153.3	173.7	200.4	231.6	151.9	149.6	247.4	164.7	191.5	270.5	175.7	208.9	275.0	188.4
Length range	81–292	111–238	113–314	92–390	138–386	124–188	120–220	137–410	117–421	125–349	152–420	121–247	144–347	177–366	113–262
Mean no. prey	17.8	26.9	45.3	123.2	38.1	9.1	12.1	97.3	35.8	37.2	61.5	20.7	35.3	80.7	35.3
Mean wt. prey	1.46	0.57	1.15	1.40	2.28	0.59	0.50	2.85	0.91	1.23	5.35	1.16	0.70	0.88	1.54

* Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

Many invertebrate prey also occurred frequently or were important numerically in the diet of juvenile coho salmon, but were much less important than fish by weight (Appendix Table 1). Principal invertebrate prey were *Cancer* crab megalopae, the hyperiid amphipods *Hyperoche medusarum* and *Themisto pacifica*, the euphausiids *Thysanoessa spinifera* and *Euphausia pacifica*, and the pteropod *Limacina helicina*. Numerous other species of decapod larvae and amphipods were eaten, as well as copepods and insects, but were of lesser importance. Juvenile *Loligo* squid were also important prey by weight.

Temporal variations Some between-cruise variability in the weight composition of the major food categories was evident (Table 2). During June 1980, coho salmon consumed mainly fishes, although cephalopods were relatively important compared with other cruises. Except during July, fishes dominated the diet during 1981. Pteropods, mainly *L. helicina*, comprised over one-half the total weight of prey in July 1981. Fishes (mostly *A. hexapterus* and *E. mordax*) and euphausiids (mainly *T. spinifera*) dominated the diet during 1982. During 1983 and 1984, coho salmon juveniles fed more upon decapod larvae than during most other years (Table 2). Several anomalous prey items of more southerly origin appeared in the diet in 1983 and 1984, including the euphausiid *Nyctiphanes simplex*, the pteropod *Euclio pyrimidata*, and the hyperiid amphipod *Vibilia* spp. The greatest number of major prey categories were found during July 1984 when terrestrial insects made up over a third of the biomass found in the coho salmon stomachs. One large lepidopteran, *Choristoneura occidentalis*, comprised greater than 37% of the total prey IRI. The diet during June 1985 resembled that of June 1982 at both the specific and general taxonomic levels.

Based on the percent of IRI for the major prey categories, juvenile coho salmon diets changed somewhat as the summer progressed (Fig. 3). Fishes were the main prey during May, although decapod larvae and pteropods were important numerically. During June, fishes and decapod larvae were the primary prey, with amphipods and euphausiids of relatively minor importance. By July and August, fish consumption decreased substantially, and pteropods and euphausiids were the major taxa consumed. Fishes were again the dominant food in September, but their importance was based mainly on weight because individual fish in the stomachs were comparatively larger. In September, pteropods, euphausiids, and amphipods were important prey numerically.

Geographic variations Diets of juvenile coho salmon in the three geographic areas were similar in that the same major prey categories were represented, despite differences in mean size of salmon among the regions. Fishes, decapod larvae, euphausiids, pteropods, and

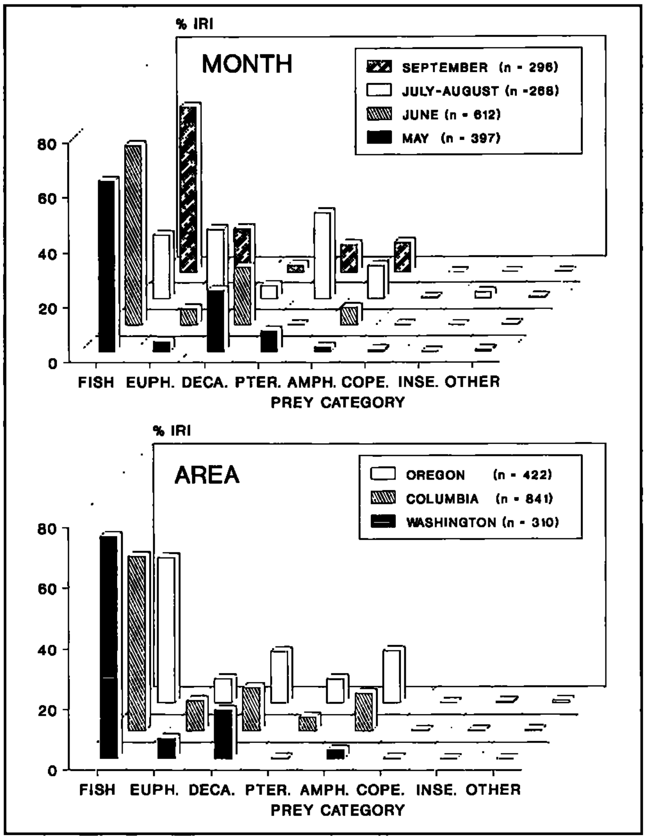

Figure 3
Juvenile coho salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

amphipods were the dominant prey in each area based on IRI proportions (Fig. 3). The relative proportions of the major prey categories were similar among the regions, although fishes were more important off Washington.

Few differences were observed among the three regions even at the lowest taxonomic levels. *Engraulis mordax* and *Sebastes* spp. were the dominant fish prey by weight in all three regions. The Washington area differed somewhat from the other regions in that *Cancer* larvae were the dominant invertebrate taxa numerically, whereas *L. helicina*, *T. spinifera*, and *H. medusarum* were dominant in the other regions.

Chinook salmon

General food habits Fishes dominated the diet of juvenile chinook salmon, occurring in over 85% of the stomachs that contained food ($n = 795$), and accounting for almost 87% of the total IRI for all years combined (Appendix Table 1). The overall mean stomach fullness (2.8) and digestion (2.3) states were similar to that of coho. Also resembling the diet of coho salmon, the main fish prey identified were *E. mordax*, *Sebastes* spp., and *A. hexapterus*, but cottid juveniles (*Hemilepidotus spinosus*) were also frequently eaten. Pleuronectid and agonid larvae were more common in the diets of juvenile chinook salmon.

Many invertebrate species were also represented in juvenile chinook salmon diets. The relative importance of the various invertebrate taxa was similar to that found for coho salmon. Decapod larvae, euphausiids, and hyperiid amphipods were the dominant invertebrate groups consumed. The dominant species in these prey categories were *C. oregonensis* megalopae, *T. spinifera*, and *H. medusarum*, respectively (Appendix Table 1). Copepods and mysids were generally more important, and pteropods and insects less important, in comparison with juvenile coho salmon.

Temporal variations Between-cruise variability in the consumption of the major prey taxa was less pronounced for chinook salmon than for coho salmon (Table 3). Fishes comprised 75% or more of the biomass consumed during every cruise, with the exception of July 1981 when euphausiids and pteropods were also major prey. The only other invertebrate taxa to contribute substantially in other cruises were cephalopods (May and June 1981), euphausiids (May 1982 and July 1984) and decapod larvae (May and June 1983). In contrast to the diet of coho salmon, insects were unimportant during July 1984 (Table 3).

Seasonally, the relative IRI proportions of fishes, decapod larvae, and euphausiids were similar for chinook salmon (Fig. 4). The diets contained more major prey categories during July–August when small zooplankton prey (copepods, pteropods, decapod larvae, and hyperiid amphipods) were important numerically. This may be due to the smaller mean size of chinook salmon collected this period; in July–August, there was an influx of subyearling chinook salmon into the sampling area. Fishes were again the dominant prey in September, although hyperiid amphipods remained important numerically.

Geographic variations The feeding patterns of juvenile chinook salmon were fairly consistent by major taxonomic categories among the three regions (Fig. 4). Fishes were the major prey by frequency of occurrence and weight in all three geographic areas, although the dominant species varied somewhat. Off Washington, *A. hexapterus*, *Sebastes* spp., and *H. spinosus* were the main fish prey consumed. *Engraulis mordax* and *H. spinosus* were the dominant prey in the Columbia region, whereas *E. mordax* dominated the diet off Oregon (>65% of the total IRI).

Table 3

Food habits by percent weight of major food categories for chinook salmon, by cruise, off Oregon and Washington.

	1980	1981				1982			1983			1984			1985
	June	May	June	July	Aug.	May	June	Sept.	May	June	Sept.	June	July	Sept.	June
Prey category															
Fishes	92.7	84.5	75.4	38.6	97.3	81.9	94.7	91.9	89.0	80.4	98.2	89.5	75.0	88.5	87.8
Euphausiids	0.1	4.1	0.3	32.7	0.6	13.2	0.4	0.6	1.1	0.1	<0.1	0.1	10.0	6.8	6.3
Decapods	0.4	2.8	8.8	6.9	0.3	3.9	3.1	<0.1	9.4	13.8	0.4	5.2	6.2	2.3	4.9
Hyperiids	—	<0.1	<0.1	3.3	0.5	0.6	<0.1	3.6	<0.1	0.4	0.5	0.2	2.5	1.5	0.3
Pteropods	—	0.1	<0.1	10.6	0.4	0.1	<0.1	—	0.1	<0.1	—	—	—	<0.1	—
Copepods	0.4	<0.1	<0.1	0.4	0.5	<0.1	<0.1	—	<0.1	0.6	<0.1	2.9	5.8	—	<0.1
Insects	—	<0.1	0.8	0.2	<0.1	—	—	0.6	—	—	<0.1	—	—	0.6	<0.1
Cephalopods	—	7.7	14.1	—	—	0.9	—	3.1	0.1	3.6	0.4	1.2	—	0.1	0.3
Other*	6.2	—	0.2	6.9	0.3	<0.1	<0.1	—	<0.1	—	0.5	0.2	0.6	0.1	0.5
Predator characteristics															
No. stomachs	14	63	32	53	32	121	112	10	95	27	89	60	21	37	74
No. empty	0	7	2	6	2	5	2	0	3	2	1	11	2	3	3
Mean length	232.5	181.8	196.5	152.9	165.0	218.9	203.7	322.9	192.6	205.7	220.3	182.2	147.2	215.1	209.9
Length range	189–283	126–290	110–331	87–347	120–347	123–400	119–350	134–435	118–396	124–287	129–325	105–370	109–251	138–412	101–354
Mean no. prey	14.6	27.8	19.0	17.0	37.4	10.8	9.4	12.0	17.1	16.0	13.7	21.9	17.4	12.3	19.2
Mean wt. prey	1.85	1.23	1.47	0.44	0.37	2.44	1.50	1.14	0.99	0.78	3.22	0.98	0.27	0.75	0.85

* Includes polychaetes, chaetognaths, gammarids, isopods, cumaceans, cirripedes, mysids, and gelatinous zooplankton.

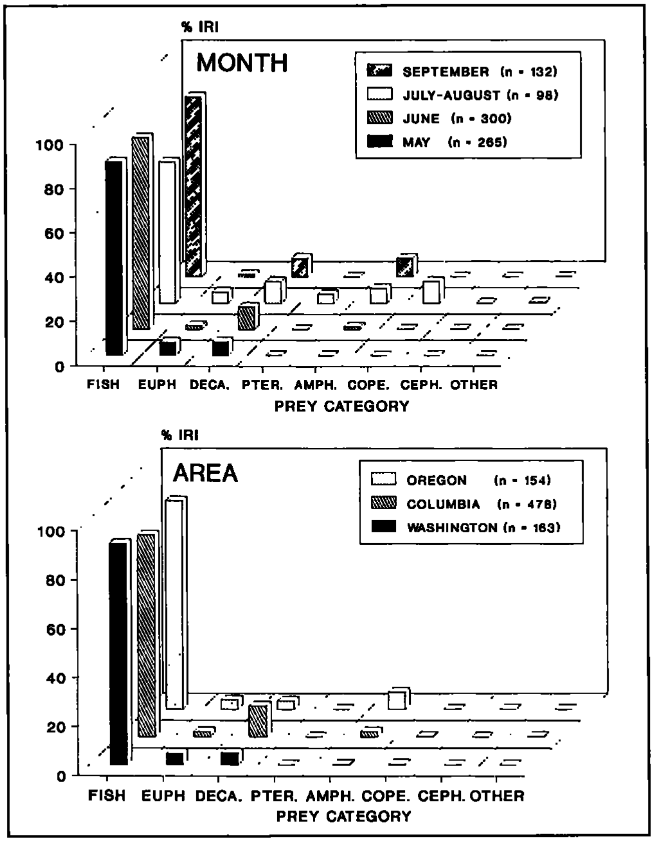

Figure 4

Juvenile chinook salmon diets by month and area for the major prey categories as a percent of total IRI. Sample sizes (no. of fish with food) for each subset are given in the legend. All figures include data collected off Washington and Oregon, 1980–85.

There were few consistent patterns observed among the invertebrate taxa consumed between the different areas (Fig. 4). Hyperiid amphipods were rarely found in chinook salmon stomachs collected off Washington as opposed to the other regions. The large numbers of decapod larvae eaten off the Columbia River were mainly *C. oregonensis* and *C. magister* larvae.

Chum salmon

General food habits Of the 109 chum salmon stomachs examined, 101 (92.6%) contained food; however, overall mean stomach fullness (2.4) and digestion (2.1) were low. The diet was dominated by zooplanktonic crustaceans, particularly euphausiids, calanoid copepods, and hyperiid amphipods (Appendix Table 2). Euphausiids (mostly juvenile *E. pacifica* and *T. spinifera*) accounted for over 54% of the total weight and 47% of the total IRI for all cruises combined. A taxonomically diverse array of hyperiids, copepods, and decapod larvae were also consumed. These taxa frequently occurred in the stomachs and were important numerically, but were of lesser importance gravimetrically. Chaetognaths and larvae and juveniles of several fish species were the dominant non-crustacean prey (Appendix Table 2).

Temporal variations Chum salmon diets varied considerably during the 5 years examined (Table 4). Some

Table 4
Summary of food habits by percent weight of major prey categories for juvenile chum salmon, by year, off Oregon and Washington.

	1981	1982	1983	1984	1985
Prey category					
Fishes	1.1	–	15.4	57.2	24.1
Euphausiids	78.3	60.7	20.5	13.7	33.0
Decapods	<0.1	8.6	1.0	–	2.0
Hyperiids	4.8	7.8	1.0	1.5	0.7
Pteropods	0.8	<0.1	–	–	–
Copepods	6.0	21.4	1.0	3.8	36.6
Chaetognaths	1.9	1.4	60.1	17.5	2.2
Other*	–	<0.1	0.9	6.1	1.3
Predator characteristics					
No. stomachs	24	33	15	8	29
No. empty	2	1	0	1	4
Mean length	190.6	161.6	116.2	165.4	132.2
Length range	108–237	97–223	103–133	126–214	115–155
Mean no. prey	47.4	8.0	78.1	20.1	83.4
Mean wt. prey	0.69	0.04	0.23	0.19	0.22

*Includes polychaetes, ostracods, mysids, insects, and larvaceans.

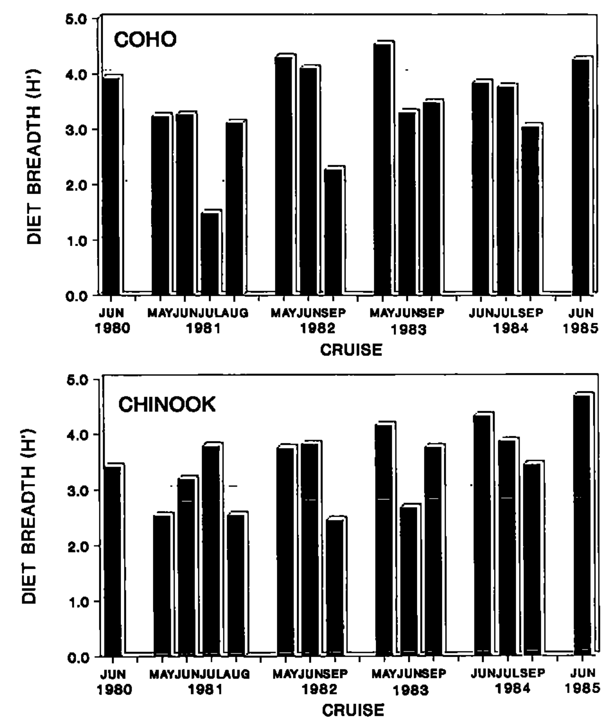

Figure 5
Shannon-Weaver niche breadth (H') values for juvenile coho and chinook salmon for each cruise period.

Table 5
Total number of prey taxa, Shannon-Weaver niche breadth (H'), maximun niche value (H'_{max}), and evenness (E) for each salmon species off Oregon and Washington, for all samples combined.

Species	Total number of prey taxa	H'	H'_{max}	E
Coho salmon	157	4.55	7.29	0.62
Chinook salmon	136	5.06	7.09	0.71
Chum salmon	51	4.35	5.67	0.77
Sockeye salmon	36	2.74	5.17	0.53

of this may be due to the months and areas sampled in different years. Euphausiids were the main food item by weight during 1981 and 1982. Although euphausiids were important during the later years, their contribution to the diet was less compared with chaetognaths, larval fishes, and calanoid copepods.

Sockeye salmon

General food habits The diet of juvenile sockeye salmon was similar to that of chum salmon. Juvenile euphausiids, calanoid copepods, chaetognaths, and fish larvae were consumed by the small number of fish examined (Appendix Table 2). Although a large number of prey taxa were identified, only a few were important. Among these were the euphausiid *T. spinifera* and larval osmerid fishes. Chaetognaths were found in substantial numbers but were well digested and not identifiable to species. The relatively small sample size of sockeye salmon stomachs precluded a detailed analysis of diet variability.

All salmon species

Niche breadth Niche breadths, maximum possible niche breadths, and evenness values are given for each salmon species in Table 5. Chinook salmon had the highest overall diversity of prey taxa (H' = 5.06), which was consistent with the high numbers of prey taxa found per stomach, and a high evenness ratio. Coho and chum salmon also consumed a diverse array of prey taxa, although coho stomachs frequently contained small numbers of prey items and showed low evenness overall. Chum salmon had a high diversity (H' = 4.35), despite a substantial amount of unidentified and digested prey, and had the highest evenness (0.77) of all salmon species. The overall prey diversity of sockeye salmon was quite low (H' = 2.74), which may be due in part to the small sample size and advanced state of digestion (mean digestion code = 2.0) of prey which prevented identification to lower taxonomic levels.

Table 6

Diet overlap by weight among all salmon species off Oregon and Washington, for all cruises combined.

Species	Coho	Chinook	Chum	Sockeye
Coho	—			
Chinook	54	—		
Chum	26	16	—	
Sockeye	25	24	33	—

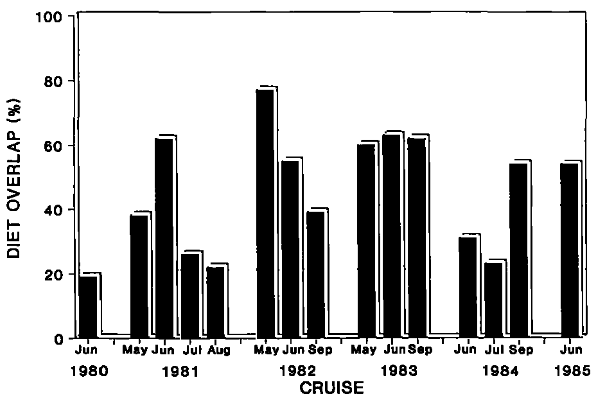

Figure 6

Diet overlap between juvenile coho and chinook salmon for each cruise period, 1980–85.

Table 7

Diet overlap by weight between juvenile coho and chinook salmon for collections off Oregon and Washington from which 10 stomachs of each species were examined. Also shown are the intraspecific overlap values for the same species at adjacent stations collected on the same day.

Date	Location	Distance offshore (km)	PSI Both	PSI Coho	PSI Chinook
1982					
June 1	45°00′, 124°05′	6.1	57		
1	44°41′, 124°24′	18.0	69		
7	47°00′, 124°25′	18.5	53		
8	46°41′, 124°18′	17.4	47	18	40
8	46°41′, 124°29′	31.8	49		
10	46°30′, 124°25′	27.6	45	38	31
10	46°30′, 124°18′	18.3	33		
1983					
Sept. 20	45°40′, 124°03′	8.9	91		
22	45°20′, 124°01′	3.7	62	59	61
22	45°17′, 124°01′	3.7	68		
1984					
June 8	47°00′, 124°25′	18.3	5		
1985					
June 18	46°19′, 124°11′	9.0	56		
25	47°40′, 124°53′	37.3	15		

Prey diversity varied greatly among cruises for juvenile coho (Fig. 5). Generally lower values occurred during 1981, especially in July, when pteropods were very important in the diet. Coho salmon had higher diversity values in 1983 and 1984 than in 1981. Chinook salmon showed many of the same interannual and seasonal trends in prey diversity as coho salmon, except that prey diversity was not appreciably lower in 1981 (Fig. 5).

Dietary overlap Diet overlap by weight among the salmon species for all cruises combined was generally low, with none of the six species pairs showing significant (>60%) overlap (Table 6). The diets of juvenile coho and chinook salmon were most similar (PSI = 54%), reflecting their common foraging on many of the same euphausiid, larval decapod, and fish species. Chum salmon diets showed the least similarity to the other species, which may be a function of the poor digestive state of the stomach contents of this species.

To examine the finer-scale variability in diet similarity between coho and chinook salmon juveniles, diet overlap was calculated for each cruise month (Fig. 6). With the exception of 1983, which showed the highest overall similarity, monthly overlap values were highly variable within years containing more than one cruise. No consistent patterns were observed between years for the same months.

A wide range of diet overlap values was observed for the 13 collections from which 10 stomachs of coho and chinook were analyzed (Table 7). Overlap was highest in the collections from September 1983, due mainly to the common utilization of *E. mordax* and several hyperiid amphipod species. Intermediate overlaps were generally observed during June 1982, resulting mainly from consumption of the same euphausiid species by both predators. There appeared to be no relationship between diet overlap and the inshore-offshore location of the collection. Diet overlap between juvenile coho and chinook at a particular station was generally higher than intraspecific overlap for either species at adjacent stations (Table 7).

Analysis of dietary variations The contingency table analysis for presence or absence of the four most-commonly-occurring major prey categories showed that there were generally highly significant variations ($P \leq 0.001$) in diets of coho and chinook juveniles by

Table 8
Results of the chi-square analysis analyzing each factor independently of the other two for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. Degrees of freedom are in parentheses below each factor.

Prey category	Year† (3)	Month (3)	Area (2)
Coho salmon			
Fishes	75.32***	83.38***	51.54***
Euphausiids	31.19***	106.38***	10.71**
Decapods	39.48***	38.42***	7.80*
Amphipods	74.61***	53.21***	2.79 n.s.
Chinook salmon			
Fishes	68.25***	65.95***	2.51 n.s.
Euphausiids	33.03***	3.15 n.s.	15.48***
Decapods	46.92***	49.15***	5.96 n.s.
Amphipods	14.36**	60.71***	13.15**

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$
†Tested for 1981–84 only.

Table 9
Results of the chi-square analysis analyzing inshore-offshore variations for major prey categories of juvenile coho and chinook salmon off Oregon and Washington. All significances are at 2 degrees of freedom.

Prey category	Coho salmon		Chinook salmon	
	May 81	June 84	May 82	June 85
Fishes	3.86 n.s.	5.82 n.s.	1.34 n.s.	1.40 n.s.
Euphausiids	3.14 n.s.	2.66 n.s.	1.82 n.s.	9.76**
Decapods	3.83 n.s.	15.07***	9.00*	1.82 n.s.
Amphipods	3.14 n.s.	15.88***	3.23 n.s.	0.41 n.s.

*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, n.s. $P > 0.05$

year and month (Table 8). The only comparison which showed non-significant variation by year or month was the monthly variation in euphausiid occurrences for juvenile chinook salmon. Three prey categories did not show significant variation ($P > 0.05$) when analyzed by area. Comparisons by area showed less significant variation than by year and month for both coho and chinook salmon juveniles for most of the major prey categories (Table 8).

Examination of inshore-offshore variations in major prey composition for four cruises (two each for coho and chinook salmon) showed generally few significant variations by occurrence for the dominant prey categories (Table 9). Although the species and life-history-stage composition of the prey was different in inshore and offshore collections (i.e., more *Sebastes* and *Engraulis* larvae offshore, and more juvenile *Ammodytes*, *Clupea*, and *Hemilepidotus* inshore), all cross-shelf variations in total fish occurrences were not significant ($P > 0.05$). The most significant differences were for decapod larvae, and were due to higher occurrences of *Cancer* spp. megalopae in chinook salmon stomachs inshore in May 1982 and lower occurrences in coho salmon stomachs inshore in June 1984.

Discussion

Overall food habits

This study represents the first detailed description of the diets of several species of sympatric juvenile salmon in coastal marine waters off Washington and Oregon. Despite generally low diet overlaps at the lowest taxonomic levels, there were some similarities in the major prey groups consumed by the salmon species. Juvenile chinook salmon were primarily piscivorous, consuming a variety of larval and juvenile fishes. The diet of coho salmon consisted of both fishes and large zooplanktonic crustaceans, such as euphausiids, crab megalopae, and hyperiid amphipods. Chum and sockeye salmon diets were more diverse than the diets of coho and chinook salmon, with fishes, small crustaceans (euphausiid furcilia and juveniles, crab larvae, and copepods), and chaetognaths being important prey.

Our findings are consistent with what is known of the marine food habits of juvenile salmon off Washington and Oregon and British Columbia. Juvenile chinook salmon tend to be more piscivorous than juvenile coho for the same-sized predator (Healey 1978, 1980; Peterson et al. 1982; Emmett et al. 1986). Coho collected during this study, however, consumed a larger overall mean length of fish prey relative to predator length (Brodeur In press). Juvenile northern anchovy, Pacific sand lance, and rockfishes were the dominant fish species eaten off Washington and Oregon (Peterson et al. 1982, Emmett et al. 1986), and herring and Pacific sand lance were the main fish species consumed off British Columbia (Healey 1978, 1980). Many of these prey fish species tend to be heavily pigmented and are often associated with the neustonic layer in coastal waters (Brodeur et al. 1987b, Shenker 1988, Brodeur 1989).

Macrozooplankton, such as euphausiids, hyperiid amphipods, and crab larvae, are also readily consumed by these juvenile salmon. These macrozooplankton prey may be easily detected due to their large size or darkly-pigmented eyes (Peterson et al. 1982) and occur in large aggregations near the surface (Brodeur et al. 1987b, Shenker 1988). Terrestrial insects, which may be blown to sea in large numbers during favorable meteorological conditions, can also contribute substantially to the diets of juvenile coho salmon and other salmonids (Brodeur 1989).

Fishes were much less important in the diets of juvenile chum and sockeye salmon; however, the mean and maximum size of the individuals of these species examined in this study were smaller than those of coho and chinook salmon. Juvenile euphausiids were a major component in the diet of chum and sockeye salmon in this study. Peterson et al. (1982) found juvenile euphausiids were a major prey of chum juveniles off Oregon, whereas copepods, larvaceans, and hyperiid amphipods were most important off British Columbia (Manzer 1969; Healey 1978, 1980). Both chum and sockeye consumed a greater number of chaetognaths than coho and chinook, and the importance of these and other soft-bodied prey may be greatly underestimated in most studies because they are probably digested very rapidly in salmon stomachs (Black and Low 1983).

Patterns in dietary variability

The pronounced interannual differences in the diets of most species were expected, even when the collections from same months and areas were examined. Oceanographic conditions varied greatly among the years, with both relatively strong (1982 and 1985), weak (1983 and 1984), and highly variable (1981) upwelling occurring during the study period (Fisher and Pearcy 1988). In addition, a strong El Niño event dominated ocean conditions in coastal waters of the northeast Pacific during the summer months of 1983 and 1984, greatly affecting primary and secondary productivity and fish production (Mysak 1986, Pearcy and Schoener 1987).

Fish prey, as a proportion of the total diet by weight, was generally invariant for the same months among the different years. However, the species composition alternated between coastal and offshore taxa (as identified by Richardson and Pearcy [1977]) depending on the prevalent hydrographic regime in the various years. Several coastal taxa (*Ammodytes hexapterus*, *Clupea harengus pallasi*, *Hemilepidotus spinosus*, and Osmeridae) were more prevalent during strong upwelling years, whereas offshore taxa (*Engraulis mordax*, *Sebastes* spp., *Ronquilus jordani*, and pleuronectid larvae) were eaten more frequently during poor upwelling years. Although ichthyoplankton collections were not made during every year of the stomach sampling, one limited study lends support to our diet observations. In a series of plankton tows along one transect off the central Oregon coast in 1983, Brodeur et al. (1985) found high abundances of offshore fish taxa at inshore stations compared with past studies. The larvae of the northern anchovy were unusually abundant that year, and juvenile anchovy made up the majority of the diet-by-weight of juvenile coho and chinook salmon during September 1983. Osmerid larvae, generally the dominant larvae inshore off Oregon (Richardson and Pearcy 1977), were found in low abundance in both the plankton collections and fish stomachs during 1983.

Several invertebrate taxa showed substantial interannual variation. The pteropod *L. helicina* was one of the most important prey consumed in 1981, but was relatively unimportant in other years. The dominant inshore euphausiid *T. spinifera* was extremely abundant in the stomachs following periods of active upwelling, but was rarely consumed during the El Niño of 1983 and early 1984 (Brodeur 1986). Several species of decapod larvae were present in greater numbers in the diets of all salmon species during 1983 and early 1984. Many other El Niño-related anomalies that were observed in the diet of coho salmon during 1983 were described by Pearcy et al. (1985). The diets of coho salmon during 1984 showed above-average abundances of terrestrial insects, which presumably were blown offshore by anomalous winds during the summer of 1984 (Brodeur 1989).

Strong seasonal variations in feeding habits of juvenile coho and chinook salmon were evident in the years that had multiple cruises over the 5-month sampling period. Some of the variability may have been due to the seasonal increase in the mean size of the salmon, which allowed a greater size range of prey to be consumed later in the summer (Brodeur In press). However, much of the diet variation may have been due to seasonal variations in the abundance of meroplanktonic prey (e.g., decapod and fish larvae). The timing and duration of spawning, larval development, and settlement to benthic juvenile habitat are relatively fixed for most meroplanktonic species (Lough 1975, Richardson and Pearcy 1977, Parrish et al. 1981) such that their seasonal occurrence in the plankton and the diets of juvenile salmon are relatively predictable. Exceptions may occur during anomalous years such as during an El Niño (Bailey and Incze 1985, Brodeur et al. 1985). Several of the major holoplanktonic taxa (e.g., euphausiids, hyperiids, and pteropods) also showed a consistent seasonal succession of developmental stages, but many species were present throughout the summer period (Brodeur 1990).

It was not surprising that geographic (north-south) variations in the diet composition of most salmon species were not as substantial as temporal variations, because most of the prey species are distributed throughout the range of latitudes we sampled. Similar results were found for adult salmonids and nonsalmonid species by Brodeur et al. (1987a). However, oceanographic regimes may be quite variable between regions (Brodeur and Pearcy 1986), which could result in different feeding conditions for juvenile salmonids within each region. The Columbia River region may be quite different hydrographically and biologically from the upwelling regions off Washington and Oregon due to the presence of a warm, low-salinity plume extending over much of the Columbia River area during the summer. Oceanic species (e.g., *Sebastes* spp., *E. pacifica*) rarely occurred in the stomachs collected from the Columbia region, whereas *E. mordax*, a species whose northern subpopulation spawns within the relatively stable Columbia River plume (Richardson 1980), was generally well represented in salmon stomachs collected in this region.

The relatively minor cross-shelf variations in the major prey taxa consumed by coho and chinook were not expected, considering that many studies have found substantial variations in cross-shelf species distributions (Peterson and Miller 1976, Richardson and Pearcy 1977, Richardson et al. 1980, Shenker 1988). However, the frequency of occurrence of major prey may not be a representative measure of the diet from a particular area. The larvae of many meroplanktonic taxa (e.g., *Sebastes* spp., *Hemilepidotus* spp., and *Cancer* spp.) are generally found offshore and progressively migrate or are transported inshore as they grow prior to settling to an inshore benthic habitat as juveniles (Richardson et al. 1980, Shenker 1988). Euphausiids consumed in our inshore study area were mainly *T. spinifera*, whereas *E. pacifica* were consumed in the offshore area. These euphausiid species have little overlap in distribution (Hebard 1966). Hyperiid amphipods were also represented by an inshore species, *Hyperoche medusarum*, and an offshore species, *T. pacifica* (Lorz and Pearcy 1975). These and other cross-shelf species differences were not detectable when analyzing stomach contents at higher taxonomic levels. However, species-level distinctions may be irrelevant to a foraging predator, if the size, energy content, and behavior of both prey species are similar.

The high prey-diversity and generally high niche-breadth values agree with previous studies which indicate that many of these salmon species are not specialists in their oceanic feeding modes, but rather consume any available prey within the proper size-range. Many of the same geographic, interannual, and seasonal patterns found in the feeding habits of the adult salmonids and pelagic nonsalmonid species (Brodeur et al. 1987a) were found in our study. These similar patterns suggest that the zooplankton and ichthyoplankton population cycles, which are intricately coupled to seasonal production cycles, may be important determinants of the feeding ecology of these salmon species. The ability to switch to alternate prey, when preferred prey are limiting, may be an important factor in the marine survival of salmon.

The high overlaps between coho and chinook juveniles seen for some cruises or individual collections may signify that some competition for prey may be occurring. This interaction could be particularly acute since coho and chinook exhibit a high degree of spatial overlap in their distributions (Pearcy and Fisher In press). This would be conceivable only if prey resources were limiting.

Because of the highly opportunistic feeding mode of most salmonids and the substantial heterogeneity in the physical and biological environment, a large-scale study over extended time-periods may be necessary to adequately describe the feeding dynamics of juvenile salmon. Major departures from the long-term mean oceanographic conditions, as exemplified by an El Niño event, can strongly affect the feeding ecology of many pelagic planktivores. Fulton and LeBrasseur (1985) have hypothesized that a northward shifting of the Subarctic Boundary from its normal position intersecting the coast off Oregon or northern California to well above Vancouver Island, British Columbia, as occurs in El Niño conditions, may expose salmon and other pelagic predators to a novel suite of available prey, with a corresponding downward shift in prey size. Grover and Olla (1987) found that a smaller mean size of copepod was consumed by larval sablefish *Anoplopoma fimbria* during the El Niño year of 1983 than during 1980, a year of relatively normal oceanographic conditions.

Our study also demonstrated anomalies in species composition in the diet during 1983 and early 1984 compared with other years; relatively large northern euphausiids were replaced by much smaller decapod larvae (i.e., Graspidae, Porcellanidae, and Pinnotheridae) and euphausiids (*Nyctiphanes simplex*) of southern origin (Brodeur 1986). Similar interannual shifts were seen in the fish prey-size spectrum consumed by coho and chinook salmon juveniles with generally smaller prey consumed during 1983 and 1984 (Brodeur In press). Consumption of smaller prey must be balanced by consumption of a greater number of prey of equivalent caloric content in order to maintain the similar growth rates seen for coho salmon during the early summers of 1983 and 1984 as non-Niño years (Fisher and Pearcy 1988). Unless prey are more aggregated during El Niño years, smaller prey would require a substantial increase in time and energy spent foraging, relative to time spent avoiding predators. This increased foraging time, at the expense of predator avoidance, may have led to the low coho and chinook salmon survival in the ocean during the El Niño years (Johnson 1988).

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Citations

Bailey, K.M., and L.S. Incze
1985 El Niño and the early life history and recruitment of fishes in temperate marine waters. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 143–165. Wash. Sea Grant Publ. WSG-WO 85-3, Univ. Wash., Seattle.

Bax, N.J.
1983 Early marine mortality of marked juvenile chum salmon (*Oncorhynchus keta*) released into Hood Canal, Puget Sound, Washington, in 1980. Can. J. Fish. Aquat. Sci. 40:426–435.

Black, E.A., and C.J. Low
1983 Ctenophores in salmon diets. Trans. Am. Fish. Soc. 112:728.

Brodeur, R.D.
1986 Northward displacement of the euphausiid *Nyctiphanes simplex* Hansen to Oregon and Washington waters following the El Niño event of 1982–83. J. Crust. Biol. 6:686–692.
1989 Neustonic feeding by juvenile salmonids in coastal waters of the Northeast Pacific. Can. J. Zool. 67:1995–2007.
1990 Abundance and distribution patterns of zooplankton along the Oregon and southern Washington coasts during the summer of 1981. Fish. Res. Inst. Publ. FRI-UW-9003, Univ. Wash., Seattle, 33 p.
In press Ontogenetic variations in the type and size of prey consumed by juvenile coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon. Environ. Biol. Fishes.

Brodeur, R.D., and W.G. Pearcy
1986 Distribution and relative abundance of pelagic non-salmonid nekton off Oregon and Washington, 1979–84. NOAA Tech. Rep. NMFS 46, 85 p.
1987 Diel feeding chronology, gastric evacuation and estimated daily ration of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), in the coastal marine environment. J. Fish. Biol. 31:465–477.

Brodeur, R.D., D.M. Gadomski, W.G. Pearcy, H.P. Batchelder, and C.B. Miller
1985 Abundance and distribution of ichthyoplankton in the upwelling zone off Oregon during anomalous El Niño conditions. Estuarine Coastal Shelf Sci. 21:365–378.

Brodeur, R.D., H.V. Lorz, and W.G. Pearcy
1987a Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. NOAA Tech. Rep. NMFS 57, 32 p.

Brodeur, R.D., W.G. Pearcy, B.C. Mundy, and R.W. Wisseman
1987b The neustonic fauna in coastal waters of the Northeast Pacific: Abundance, distribution, and utilization by juvenile salmonids. Oreg. Sea Grant Coll. Prog. Publ. ORESU-T-87-001., Oreg. State Univ., Corvallis, 61 p.

Emmett, R.L., D.R. Miller, and T.H. Blahm
1986 Food of juvenile chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon off the northern Oregon and Southern Washington coasts, May–September 1980. Calif. Fish Game 72:38–46.

Fisher, J.P., and W.G. Pearcy
1985 Studies of juvenile salmonids off the Oregon and Washington coast, 1985. Oreg. Sea Grant Coll. Prog. Publ. ORESU-T-85-004, Oreg. State Univ., Corvallis, 31 p.
1988 Growth of juvenile coho salmon (*Oncorhynchus kisutch*) in the ocean off Oregon and Washington, USA in years of differing coastal upwelling. Can. J. Fish. Aquat. Sci. 45: 1036–1044.

Fulton, J.D., and R.J. LeBrasseur
1985 Interannual shifting of the Subarctic Boundary and some of the biotic effects on juvenile salmonids. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 237–247. Wash. Sea Grant Publ. WSG-WO 85-3, Univ. Wash., Seattle.

Furnell, D.J., and J.R. Brett
1986 Model of monthly marine growth and mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43:999–1004.

Grover, J.J., and B.L. Olla
1987 Effects of an El Niño event on the food habits of larval sablefish, *Anoplopoma fimbria*, off Oregon and Washington. Fish. Bull., U.S. 85:71–79.

Gunsolus, R.T.
1978 The status of Oregon coho and recommendations for managing the production, harvest, and escapement of wild and hatchery-reared stocks. Oreg. Dep. Fish. Wildl., Fish Div. Proc. Rep., 59 p.

Healey, M.C.
1978 The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Can. Fish. Mar. Serv. Tech. Rep. 788, 49 p.
1980 The ecology of juvenile salmon in Georgia Strait, British Columbia. *In* McNeil, W.J., and D.C. Himsworth (eds.), Salmonid ecosystems of the North Pacific, p. 203–229. Oreg. State Univ. Press, Corvallis.

Hebard, J.F.
1966 Distribution of Euphausiacea and Copepoda in relation to oceanographic conditions. Ph.D. thesis, Oreg. State Univ., Corvallis, 85 p.

Johnson, S.L.
1988 The effects of the 1983 El Niño on Oregon's coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon. Fish. Res. (Amst.) 6:105–123.

Linton, L.R., R.W. Davies, and F.J. Wrona
1981 Resource utilization indices: An assessment. J. Anim. Ecol. 50:283–292.

Lorz, H.V., and W.G. Pearcy
1975 Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32:1442–1447.

Lough, R.G.
1975 Dynamics of crab larvae (Anomura, Brachyura) off the central Oregon coast, 1969–1971. Ph.D. thesis, Oreg. State Univ., Corvallis, 229 p.

Mathews, S.B., and R. Buckley
1976 Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33:1677–1684.

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

McGie, A.
1984 Commentary: Evidence for density dependence among coho salmon stocks in the Oregon Production Index Area. *In* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 37–49. Oreg. Sea Grant Coll. Prog. ORESU-W-83-001, Oreg. State Univ., Corvallis.

Mysak, L.A.
1986 El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464–497.

Nickelson, T.E.
1986 Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon Production area. Can. J. Fish. Aquat. Sci. 43:527–535.

Parker, R.R.
1968 Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757–794.
1971 Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503–1510.

Parrish, R.H., C.S. Nelson, and A. Bakun
1981 Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.

Pearcy, W.G.
1984 Where do all the coho go? The biology of juvenile salmon off the coasts of Oregon and Washington. *In* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the North Pacific, p. 50–60. Oreg. Sea Grant Coll. Prog. Publ. ORESU-W-83-001, Oreg. State Univ., Corvallis.
1988 Factors affecting survival of coho salmon off Oregon and Washington. *In* McNeil, W.J. (ed.), Salmon production, management, and allocation, p. 67–73. Oreg. State Univ. Press, Corvallis.

Pearcy, W.G., and J.P. Fisher
1988 Migrations of coho salmon, *Oncorhynchus kisutch*, during their first summer in the ocean. Fish. Bull., U.S. 86: 173–195.
In press Distribution and abundance of juvenile salmonids off Oregon and Washington, 1981-1985. NOAA Tech. Rep. NMFS 93.

Pearcy, W.G., and A. Schoener
1987 Changes in the marine biota coincident with the 1982-1983 El Niño in the northeastern subarctic Pacific Ocean. J. Geophys. Res. 92:14417–14428.

Pearcy, W., J. Fisher, R. Brodeur, and S. Johnson
1985 Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. *In* Wooster, W.S., and D.L. Fluharty (eds.), El Niño North: Niño effects in the eastern subarctic Pacific Ocean, p. 188–204. Wash. Sea Grant Publ. WSG-WO 85-3, Univ. Wash., Seattle.

Peterman, R.M.
1982 Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39: 904–913.

Peterman, R.M., and R.D. Routledge
1983 Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): Designing for yield of information. Can. J. Fish. Aquat. Sci. 40:1212–1223.

Peterson, W.T., and C.B. Miller
1976 Zooplankton along the continental shelf off Newport, Oregon, 1969–1972: Distribution, abundance, seasonal cycle, and year-to-year variations. Oreg. Sea Grant Coll. Publ. ORESU-T-76-002, Oreg. State Univ., Corvallis, 111 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., U.S. 80:841–851.

Petraitis, P.S.
1979 Likelihood measures of niche breadth and overlap. Ecology 60:703–710.

Pielou, E.C.
1977 Mathematical ecology. John Wiley, NY, 385 p.

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.

Richardson, S.L.
1980 Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern sub-population off Oregon and Washington. Fish. Bull., U.S. 78:855–877.

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.

Richardson, S.L., J.L. Laroche, and M.D. Richardson
1980 Larval fish assemblages and associations in the Northeast Pacific Ocean along the Oregon coast, winter-spring 1972–1975. Estuarine Coastal Mar. Sci. 11:671–699.

Shenker, J.M.
1988 Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crabs off Oregon, 1984. Fish. Bull., U.S. 86:299–317.

Snedecor, G.W., and W.G. Cochran
1967 Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.

Wallace, R.K.
1981 An assessment of diet overlap indexes. Trans. Am. Fish. Soc. 110:72–76.

Appendix Table 1

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile coho and chinook salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Coho salmon				Chinook salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	0.3	<0.1	<0.1	<0.1	—	—	—	—
Ctenophora								
Unidentified	<0.1	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Siphonophora								
Unidentified	1.0	<0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Annelida								
Tomopteris septentrionalis	<0.1	<0.1	<0.1	<0.1	—	—	—	—
Tomopteris sp.	0.6	0.1	<0.1	<0.1	—	—	—	—
Pelagobia sp.	0.1	<0.1	<0.1	<0.1	—	—	—	—
Nereidae	—	—	—	—	0.1	<0.1	0.1	<0.1
Unidentified	0.5	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Mollusca								
Gastropoda	(18.4)	(13.4)	(5.9)		(4.1)	(1.3)	(0.3)	
Limacina helicina	16.5	13.0	5.5	10.4	4.0	1.3	0.3	0.3
Euclio pyramidata	1.5	0.3	0.5	<0.1	—	—	—	—
Clio limacina	0.1	0.1	<0.1	<0.1	—	—	—	—
Pteropoda unidentified	0.4	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Cephalopoda	(2.0)	(0.1)	(0.9)		(2.0)	(0.4)	(1.5)	
Loligo opalescens	1.0	0.1	0.8	<0.1	0.7	0.4	1.1	<0.1
Abraliopsis sp.	0.1	<0.1	<0.1	<0.1	—	—	—	—
Gonatidae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Octopus dofleini	—	—	—	—	0.2	<0.1	0.1	<0.1
Unidentified	0.8	<0.1	0.1	<0.1	0.9	<0.1	0.2	<0.1
Arthropoda								
Copepoda	(9.6)	(2.1)	(0.2)		(8.5)	(2.6)	(0.2)	
Gaussia princeps	—	—	—	—	0.1	<0.1	<0.1	<0.1
Neocalanus cristatus	3.2	0.5	0.1	<0.1	3.8	0.7	0.1	0.1
Neocalanus plumchrus	0.5	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Calanus marshallae	0.5	<0.1	<0.1	<0.1	0.2	0.1	<0.1	<0.1
Calanus pacificus	1.7	0.5	<0.1	<0.1	0.4	1.2	<0.1	0.1
Calanus spp. copepodites	0.6	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Eucalanus bungii	0.3	0.6	<0.1	<0.1	0.9	0.2	<0.1	<0.1
Metridia pacifica	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Epilabidocera longipedata	1.6	0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Euchaeta elongata	0.1	<0.1	<0.1	<0.1	—	—	—	—
Eurytemora americana	0.1	<0.1	<0.1	<0.1	—	—	—	—
Candacia bipinnata	0.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	3.4	0.2	<0.1	<0.1	2.6	0.3	<0.1	<0.1
Cirripedia								
Unidentified cypris	1.7	0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Unidentified remains	0.2	<0.1	<0.1	<0.1	—	—	—	—
Mysidacea								
Acanthomysis macropsis	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Neomysis kadiakensis	0.5	0.1	<0.1	<0.1	1.0	0.1	0.1	<0.1
Mysidopsis californica	0.1	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	0.3	<0.1	<0.1	<0.1	0.5	0.3	<0.1	<0.1
Cumacea								
Eudorella sp.	—	—	—	—	0.1	0.2	<0.1	<0.1
Unidentified	<0.1	<0.1	<0.1	<0.1	—	—	—	—
Isopoda								
Synidotea bicuspida	—	—	—	—	0.1	0.2	<0.1	<0.1
Gnorimosphaeroma oregonensis	—	—	—	—	0.1	<0.1	<0.1	<0.1
Idotea fewkesi	0.2	<0.1	<0.1	<0.1	—	—	—	—

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Amphipoda	(42.0)	(22.3)	(3.1)		(20.7)	(9.6)	(0.4)	
Atylus tridens	2.5	1.9	<0.1	0.2	2.5	2.1	<0.1	0.2
Calliopius laeviusculus	0.2	0.3	<0.1	<0.1	—	—	—	—
Cyphocaris challengeri	—	—	—	—	0.1	<0.1	<0.1	<0.1
Unidentified Gammaridea	0.3	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Hyperia medusarum	5.8	1.1	0.2	0.3	2.3	<0.1	0.1	<0.1
Hyperia spinigera	0.1	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Hyperoche medusarum	27.6	13.4	1.6	13.9	12.4	6.7	0.2	3.6
Themisto pacifica	13.7	4.2	0.6	2.2	1.9	<0.1	<0.1	<0.1
Primno brevidens	0.5	<0.1	<0.1	<0.1	—	—	—	—
Primno macropa	0.6	<0.1	<0.1	<0.1	1.5	<0.1	<0.1	<0.1
Phronima sedentaria	1.5	0.1	0.1	<0.1	0.9	<0.1	<0.1	<0.1
Paraphronima crassipes	0.3	<0.1	<0.1	<0.1	—	—	—	—
Paraphronima gracilis	0.5	0.1	<0.1	<0.1	—	—	—	—
Vibilia armata	3.6	0.2	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Vibilia australis	1.3	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia propinquus	3.1	0.1	0.1	<0.1	0.2	<0.1	<0.1	<0.1
Vibilia pyripes	0.2	<0.1	<0.1	<0.1	—	—	—	—
Vibilia viatrix	1.7	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Vibiliidae unidentified	0.8	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Streetsia challengeri	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Oxycephalus clausi	0.2	<0.1	<0.1	<0.1	—	—	—	—
Lestrigonus schizogeniosis	0.1	<0.1	<0.1	<0.1	—	—	—	—
Brachyscelus crusculum	0.5	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Unidentified Hyperiidea	10.6	0.8	0.4	0.4	3.9	0.5	<0.1	0.1
Caprella incisa	0.1	<0.1	<0.1	<0.1	—	—	—	—
Caprella verrucosa	0.1	<0.1	<0.1	<0.1	—	—	—	—
Euphausiacea	(33.7)	(15.6)	(10.2)		(18.2)	(13.0)	(4.7)	
Euphausia pacifica	10.0	1.6	3.9	1.9	2.8	0.8	0.8	0.2
Nematoscelis difficilis	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Thysanoessa spinifera	19.5	11.6	5.1	11.0	11.1	10.3	3.5	6.4
Nyctiphanes simplex	3.0	0.4	0.2	0.1	1.6	0.1	<0.1	<0.1
Unidentified furcilia	1.3	1.0	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Unidentified	11.8	1.0	1.0	0.8	5.5	1.7	0.3	0.5
Decapoda	(45.1)	(28.2)	(4.8)		(35.0)	(29.1)	(3.3)	
Hippolyte clarki	0.1	<0.1	<0.1	<0.1	—	—	—	—
Hippolytidae unidentified	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pandalus jordani	—	—	—	—	2.3	0.4	0.1	<0.1
Pandalus spp. zoea	0.3	<0.1	<0.1	<0.1	1.6	1.4	<0.1	0.1
Crangon spp. zoea	3.1	1.0	0.1	0.1	5.2	1.1	0.1	0.3
Natantia unidentified	0.5	0.1	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Callianassa sp. zoea	0.6	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Upogebia sp. zoea	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Emerita analoga	0.2	<0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pagurus granosimanus	0.1	<0.1	<0.1	<0.1	—	—	—	—
Pagurus spp. zoea	0.9	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pagurus spp. megalopae	4.4	1.0	0.1	0.2	2.6	2.4	<0.1	0.3
Petrolithes cinctipes	0.2	<0.1	<0.1	<0.1	—	—	—	—
Petrolithes eriomerus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Pachycheles pubescens	0.6	<0.1	<0.1	<0.1	0.7	0.2	<0.1	<0.1
Pachycheles rudis	0.5	0.1	<0.1	<0.1	0.2	<0.1	<0.1	<0.1
Pachycheles sp. zoea	0.2	<0.1	<0.1	<0.1	0.4	0.1	<0.1	<0.1
Porcellanidae zoea	1.4	0.1	<0.1	<0.1	0.6	0.2	<0.1	<0.1
Porcellanidae megalopae	2.5	0.4	<0.1	<0.1	2.6	0.7	<0.1	0.3
Oregonia gracilis	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Chionoecetes tanneri	0.2	<0.1	<0.1	<0.1	0.6	<0.1	<0.1	<0.1
Pugettia producta zoea	3.2	0.1	<0.1	<0.1	3.1	0.3	<0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	Coho salmon N	Coho salmon W	Coho salmon IRI	Chinook salmon F	Chinook salmon N	Chinook salmon W	Chinook salmon IRI
Arthropoda (continued)								
Decapoda (continued)								
Cancer antennarius megalopae	3.6	1.0	<0.1	0.1	2.5	1.3	0.3	0.2
Cancer magister megalopae	8.0	1.1	1.0	0.6	6.0	2.5	1.4	1.0
Cancer oregonensis megalopae	24.2	13.2	2.2	12.5	13.8	8.0	0.6	5.0
Cancer spp. zoea	8.6	5.5	0.3	1.7	1.9	0.6	<0.1	<0.1
Cancer spp. megalopae	4.1	0.4	0.2	0.1	3.3	0.3	0.2	0.1
Fabia subquadrata	0.8	0.1	<0.1	<0.1	1.1	3.3	0.1	0.2
Pinnixia sp. megalopae	0.2	<0.1	<0.1	<0.1	—	—	—	—
Pinnotheridae zoea	5.7	2.7	0.3	0.6	4.0	2.7	0.1	0.5
Pinnotheridae megalopae	2.0	0.3	0.1	<0.1	3.9	2.0	0.1	0.3
Lophopanopeus bellus	2.9	0.4	<0.1	<0.1	0.7	0.1	<0.1	<0.1
Pachygraspus crassipes	0.1	<0.1	<0.1	<0.1	—	—	—	—
Hemigraspus oregonensis	0.2	<0.1	<0.1	<0.1	—	—	—	—
Unidentified larvae	3.6	0.1	<0.1	<0.1	2.6	0.7	0.1	0.1
Unidentified Crustacea	3.2	<0.1	0.2	<0.1	1.1	<0.1	<0.1	<0.1
Insecta	(6.9)	(1.4)	(0.9)		(3.1)	(0.6)	(0.1)	
Psocoptera	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hemiptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Cicadellidae	—	—	—	—	0.1	<0.1	<0.1	<0.1
Aphididae	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Homoptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Coccinellidae	0.1	<0.1	<0.1	<0.1	—	—	—	—
Coleoptera	0.1	<0.1	<0.1	<0.1	—	—	—	—
Hemerobiidae	0.9	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Neuroptera	0.2	<0.1	<0.1	<0.1	—	—	—	—
Choristoneura occidentalis	1.3	0.4	0.8	0.1	—	—	—	—
Geometridae	0.1	<0.1	<0.1	<0.1	—	—	—	—
Lepidoptera	0.4	0.1	<0.1	<0.1	—	—	—	—
Nematocera	0.5	<0.1	<0.1	<0.1	—	—	—	—
Brachycera	0.6	<0.1	<0.1	<0.1	0.4	<0.1	<0.1	<0.1
Chironomid larvae	—	—	—	—	0.1	0.1	<0.1	<0.1
Diptera	0.5	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Formicidae	—	—	—	—	0.1	<0.1	<0.1	<0.1
Hymenoptera	0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1
Unidentified	4.1	0.7	0.1	0.1	2.4	0.1	<0.1	<0.1
Chaetognatha								
Eukhronia hamata	—	—	—	—	0.1	<0.1	<0.1	<0.1
Sagitta elegans	0.3	0.6	<0.1	<0.1	—	—	—	—
Unidentified	1.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Salpidae								
Unidentified	0.4	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chordata								
Osteichthyes	(66.7)	(15.2)	(72.0)		(85.3)	(42.1)	(88.3)	
Clupea harengus pallasi	3.4	0.1	2.5	0.3	6.3	0.3	1.8	0.5
Engraulis mordax	7.4	0.4	23.3	5.9	12.2	2.0	34.9	18.9
Allosmerus elongatus	0.2	<0.1	0.7	<0.1	0.9	<0.1	2.0	0.1
Spirinchus starksi	—	—	—	—	0.1	<0.1	0.4	<0.1
Osmeridae unidentified	3.4	0.7	1.3	0.2	5.8	0.5	2.9	0.8
Myctophidae unidentified	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Gadus macrocephalus	0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Microgadus proximus	1.7	0.1	1.6	0.1	1.8	0.7	0.6	0.1
Sebastes jordani	0.2	<0.1	0.3	<0.1	0.2	<0.1	0.3	<0.1
Sebastes spp.	14.7	2.6	13.0	7.7	11.7	2.9	8.4	5.5
Hexagrammos decagrammus	0.1	<0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Hexagrammos spp.	0.3	<0.1	0.3	<0.1	—	—	—	—
Ophiodon elongatus	0.5	<0.1	0.2	<0.1	0.6	<0.1	0.1	<0.1
Hexagrammidae unidentified	1.1	0.1	0.9	<0.1	0.4	<0.1	0.1	<0.1

Appendix Table 1 (continued)

Prey taxa	Coho salmon F	N	W	IRI	Chinook salmon F	N	W	IRI
Chordata (continued)								
Osteichthyes (continued)								
Agonopsis vulsa	—	—	—	—	0.1	<0.1	<0.1	<0.1
Odontopyxis trispinosa	—	—	—	—	1.5	0.2	<0.1	<0.1
Stellerina xyosterna	—	—	—	—	0.1	<0.1	<0.1	<0.1
Agonidae unidentified	0.1	0.1	<0.1	<0.1	0.9	<0.1	<0.1	<0.1
Cyclopteridae unidentified	0.1	0.1	<0.1	<0.1	0.6	<0.1	0.1	<0.1
Artedius fenestralis	0.1	0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
Artedius harringtoni	—	—	—	—	0.6	<0.1	<0.1	<0.1
Artedius meanyi	0.1	<0.1	<0.1	<0.1	1.0	<0.1	<0.1	<0.1
Hemilepidotus spinosus	5.8	0.2	2.2	0.5	14.0	0.8	6.8	4.5
Radulinus asprellus	0.1	<0.1	<0.1	<0.1	0.5	0.2	<0.1	<0.1
Scorpaenichthys marmoratus	0.8	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1
Chitonotus pugetensis	0.1	<0.1	<0.1	<0.1	0.2	0.2	<0.1	<0.1
Cottidae unidentified	1.3	<0.1	0.2	<0.1	4.1	3.5	0.4	0.7
Ammodytes hexapterus	9.5	2.7	4.4	2.3	13.7	4.4	4.3	5.1
Pholidae unidentified	0.1	0.1	<0.1	<0.1	—	—	—	—
Ronquilus jordani	1.6	0.8	0.6	0.1	2.5	4.5	0.4	0.5
Stichaeidae unidentified	0.1	<0.1	<0.1	<0.1	—	—	—	—
Coryphopterus nicholsi	0.1	<0.1	<0.1	<0.1	—	—	—	—
Citharichthys sordidus	0.1	<0.1	<0.1	<0.1	0.4	<0.1	0.1	<0.1
Citharichthys stigmaeus	0.2	<0.1	0.1	<0.1	1.0	<0.1	0.7	<0.1
Atherestes stomias	—	—	—	—	1.0	2.8	0.5	0.1
Eopsetta jordani	—	—	—	—	0.1	<0.1	<0.1	<0.1
Glyptocephalus zachirus	0.4	<0.1	<0.1	<0.1	1.0	<0.1	0.3	<0.1
Hippoglossoides elassodon	—	—	—	—	0.1	<0.1	<0.1	<0.1
Isopsetta isolepis	0.5	<0.1	<0.1	<0.1	3.6	0.2	0.6	0.1
Lepidopsetta bilineata	—	—	—	—	0.1	<0.1	<0.1	<0.1
Lyopsetta exilis	—	—	—	—	0.6	<0.1	0.1	<0.1
Parophrys vetulus	0.4	<0.1	0.1	<0.1	3.3	0.1	0.4	0.1
Psettichthys melanostictus	1.5	0.1	0.5	<0.1	6.7	1.6	1.9	1.0
Pleuronectidae larvae	1.6	<0.1	0.3	<0.1	7.7	0.4	1.1	0.5
Unidentified larvae	8.9	1.3	1.1	0.7	18.7	5.1	3.5	6.8
Unidentified juveniles	4.4	1.7	2.9	0.7	6.2	2.5	4.8	1.9
Unidentified remains	38.0	3.4	14.5	22.9	41.5	8.3	10.2	32.3
Plant material	3.0	0.4	0.2	0.1	1.3	<0.1	<0.1	<0.1
Unidentified material	16.9	0.2	1.2	0.8	9.1	0.1	0.7	0.3
Number of stomachs examined		1652				844		
Number of empty stomachs		79				49		
Mean fork length (mm)		193.80				200.47		
Fork length range (mm)		81–421				81–435		

Appendix Table 2

Percent frequency occurrence (F), percent number (N), percent weight (W), and percent index of relative importance (IRI) of food items in juvenile chum and sockeye salmon stomachs taken off Oregon and Washington, for all years combined. Numbers in parentheses refer to summaries for major taxonomic groupings.

	Chum salmon				Sockeye salmon			
Prey taxa	F	N	W	IRI	F	N	W	IRI
Cnidaria								
Velella velella	1.0	<0.1	0.1	<0.1	—	—	—	—
Siphonophora								
Unidentified	2.0	0.2	0.1	<0.1	—	—	—	—
Annelida								
Tomopteris spp.	—	—	—	—	16.7	0.3	2.2	1.0
Unidentified	2.0	0.3	<0.1	<0.1	—	—	—	—
Mollusca								
Gastropoda								
Limacina helicina	3.0	0.1	0.5	0.1	16.7	1.5	2.5	1.7
Arthropoda								
Ostracoda								
Unidentified	1.0	<0.1	<0.1	<0.1	—	—	—	—
Copepoda	(49.0)	(39.2)	(11.5)		(46.7)	(11.0)	(5.1)	
Calanus marshallae	4.9	0.1	0.3	0.1	3.3	<0.1	0.1	<0.1
Calanus pacificus	12.9	7.4	3.1	4.7	3.3	7.6	2.1	0.8
Calanus spp. copepodites	3.0	1.0	0.4	0.1	3.3	<0.1	0.1	<0.1
Neocalanus cristatus	10.9	2.3	1.8	1.6	10.0	0.1	0.3	0.1
Neocalanus plumchrus	7.9	0.6	0.5	0.3	20.0	1.3	0.6	1.0
Eucalanus bungii	13.9	17.0	3.8	10.0	—	—	—	—
Epilabidocera longipedata	1.0	0.8	0.1	<0.1	6.7	0.3	0.2	0.1
Unidentified	20.8	10.3	1.9	8.8	26.7	1.6	1.5	2.0
Cirripedia								
Unidentified cypris	3.0	<0.1	0.1	<0.1	—	—	—	—
Mysidacea								
Acanthomysis macropsis	1.0	0.3	0.1	<0.1	—	—	—	—
Amphipoda	(46.1)	(5.8)	(7.8)		(46.7)	(2.7)	(3.6)	
Hyperia medusarum	1.0	0.6	<0.1	<0.1	—	—	—	—
Hyperoche medusarum	27.7	2.4	3.1	5.3	36.7	1.4	2.0	3.0
Themisto pacifica	7.9	2.3	0.3	0.7	13.3	0.4	0.3	0.2
Primno macropa	1.0	0.3	<0.1	<0.1	—	—	—	—
Vibilia armata	1.0	<0.1	0.1	<0.1	—	—	—	—
Vibilia australis	—	—	—	—	3.3	0.2	0.1	<0.1
Vibilia viatrix	1.0	<0.1	0.1	<0.1	—	—	—	—
Unidentified Hyperiidea	14.8	0.2	0.8	0.5	23.3	0.7	0.9	0.9
Euphausiacea	(49.0)	(15.7)	(51.1)		(63.3)	(46.2)	(15.1)	
Euphausia pacifica	19.8	3.2	40.8	30.3	20.0	0.4	5.4	2.8
Thysanoessa spinifera	20.8	10.4	7.1	12.7	26.7	44.6	4.2	31.7
Unidentified furcilia	7.9	0.6	0.3	0.3	6.7	0.6	0.3	0.1
Unidentified remains	14.8	1.5	5.9	3.9	33.3	0.5	3.8	3.5
Decapoda	(22.5)	(12.5)	(1.3)		(25.0)	(4.9)	(4.6)	
Hippolytidae zoea	2.0	0.9	0.1	0.1	—	—	—	—
Natantia larvae	3.0	0.1	0.1	<0.1	3.3	<0.1	0.1	<0.1
Pagurus spp. megalopae	—	—	—	—	3.3	0.3	0.3	<0.1
Pugettia producta zoea	6.9	1.2	0.2	0.3	3.3	0.4	0.1	<0.1
Cancer antennarius meg.	1.0	0.6	<0.1	<0.1	3.3	<0.1	0.1	<0.1
Cancer magister meg.	1.0	<0.1	<0.1	<0.1	—	—	—	—
Cancer oregonensis meg.	5.9	3.7	0.3	0.8	—	—	—	—
Cancer spp. zoea	7.9	5.6	0.5	1.6	3.3	<0.1	0.1	<0.1
Pachycheles pubescens	—	—	—	—	3.3	1.1	1.0	0.2
Pachycheles rudis	—	—	—	—	3.3	1.0	0.1	<0.1
Porcellanid zoea	—	—	—	—	3.3	0.1	0.1	<0.1
Lophopanopeus bellus	—	—	—	—	3.3	0.1	0.1	<0.1
Pinnotherid megalopae	1.0	0.6	<0.1	<0.1	3.3	0.5	0.5	0.1
Hemigraspus oregonensis	—	—	—	—	3.3	1.1	0.5	0.1
Unidentified larvae	1.0	<0.1	<0.1	<0.1	10.0	0.2	0.4	0.1

Appendix Table 2 (continued)

Prey taxa	Chum salmon				Sockeye salmon			
	F	N	W	IRI	F	N	W	IRI
Arthropoda (continued)								
Crustacean remains	11.9	0.1	9.5	4.0	10.0	0.1	1.2	0.3
Insecta								
Diptera	1.0	<0.1	<0.1	<0.1	—	—	—	—
Unidentified	3.0	<0.1	<0.1	<0.1	—	—	—	—
Chaetognatha								
Sagita elegans	5.9	2.8	2.8	1.2	—	—	—	—
Unidentified	18.8	5.0	5.3	6.8	26.7	18.0	7.5	16.6
Chordata								
Larvacea								
Oikopleura sp.	2.0	2.4	0.4	0.2	—	—	—	—
Osteichthys	(30.4)	(15.0)	(10.4)		(56.7)	(16.2)	(58.2)	
Clupea harengus pallasi	—	—	—	—	3.3	0.2	3.1	0.3
Engraulis mordax	4.9	0.3	1.8	0.4	6.7	0.2	0.2	0.1
Osmeridae	2.0	0.6	0.6	0.1	20.0	1.1	29.0	14.7
Scorpaenichthys marmoratus	1.0	<0.1	<0.1	<0.1	—	—	—	—
Chitonotus pugetensis	1.0	0.3	0.1	<0.1	—	—	—	—
Cottidae	1.0	0.3	<0.1	<0.1	—	—	—	—
Ammodytes hexapterus	2.0	0.9	1.1	0.1	—	—	—	—
Ronquilus jordani	6.9	5.2	1.6	1.6	—	—	—	—
Unidentified larvae	7.9	3.2	1.3	1.2	16.7	14.1	9.3	9.5
Unidentified juveniles	1.0	1.4	0.3	1.0	—	—	—	—
Unidentified remains	10.9	2.9	2.1	1.9	13.3	0.5	11.3	3.8
Number of stomachs examined	109				32			
Number of empty stomachs	8				2			
Mean fork length (mm)	154.8				129.8			
Fork length range (mm)	97–237				104–149			