TYPE, QUANTITY, AND SIZE OF FOOD OF PACIFIC SALMON (*ONCORHYNCHUS*) IN THE STRAIT OF JUAN DE FUCA, BRITISH COLUMBIA

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ABSTRACT

The volume, numbers, and size of prey of sockeye, *Oncorhynchus nerka*; pink, *O. gorbuscha*; coho, *O. kisutch*; and chinook, *O. tshawytscha*, salmon were investigated for troll-caught salmon in the Strait of Juan de Fuca off southwestern Vancouver Island during 1967-68. Sockeye salmon was the least piscivorous species with only 7% of the stomach volume comprised of fish, while chinook salmon was the most piscivorous species at 56%. Sand lance, *Ammodytes hexapterus*, and euphausiids were the most important fish and invertebrate prey, respectively. As predator size increased, mean size of fish prey increased, and predators shifted to species of larger mean size. Similar results were found for the invertebrate prey, with mean number of prey consumed per predator increasing for the larger invertebrate species as predator size increased. Rate of increase in mean length of fish prey was proportional to increasing predator length. The observed increase in invertebrate size with increasing predator length was not statistically significant. Although chinook and coho salmon had similar diets, they were caught at significantly different water depths. *Oncorhynchus* species with fewer, shorter, and more widely spaced gillrakers have higher proportions of fish in their diet than species with numerous, long, and narrow set gillrakers.

The life history of Pacific salmon is quite variable among species, with fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, migrating to sea soon after emergence from the gravel, while those of sockeye salmon, *O. nerka*, coho salmon, *O. kisutch*, and chinook salmon, *O. tshawytscha*, may spend up to 2 yr in freshwater. Once in the ocean they can migrate a considerable distance from their natal streams and feed on a variety of organisms (Godfrey et al. 1975; French et al. 1976; Major et al. 1978; Takagi et al. 1981). Salmon thus move through a number of habitats during their life cycle and consume a diverse array of prey.

Food preferences of salmon in the range of habitats that they occupy have been an area of continuing investigation (Allen and Aron 1958; Prakash 1962; LeBrasseur 1966; Parker 1971; Eggers 1982). Relative amounts of different prey types eaten in varying environments have been examined, as well as preferences by different sizes of predators in relation to the size and abundance of prey. *Oncorhynchus* species differ considerably in their size, morphology, and ocean distribution (Hikita 1962; Neave et al. 1976; Takagi et al. 1981; Beacham and Murray 1983). Morphological differences and diet partitioning have been reported for many fish species (Keast and Webb 1966; Hyatt 1979), and diet partitioning may thus be expected among *Oncorhynchus* species. Prey size is related to predator size (O'Brien 1979; Gibson 1980), and differential prey selection among *Oncorhynchus* species may also be apparent.

Stomach contents of sockeye, pink, coho, and chinook salmon were investigated in a research trolling program conducted off southern Vancouver Island in the Strait of Juan de Fuca during 1967-68. The relative importance of different prey types, including fish and invertebrates, in the diet of the four species was studied with respect to prey size, predator size, predator morphology, and diet partitioning in relation to salmonid habitat and morphology.

MATERIALS AND METHODS

The salmon were obtained by test trolling in the Strait of Juan de Fuca during 19 June-11 October 1967 and 1 May-12 July 1968 (Fig. 1). Detailed methodology of the program has been outlined by Graham and Argue (1972). For each salmon sampled, date, fork length (mm), round weight, and sex were recorded. Stomachs were removed, placed in numbered cloth sample bags along with any food organisms in the mouth cavity, and preserved in 10% Formalin[2] solution.

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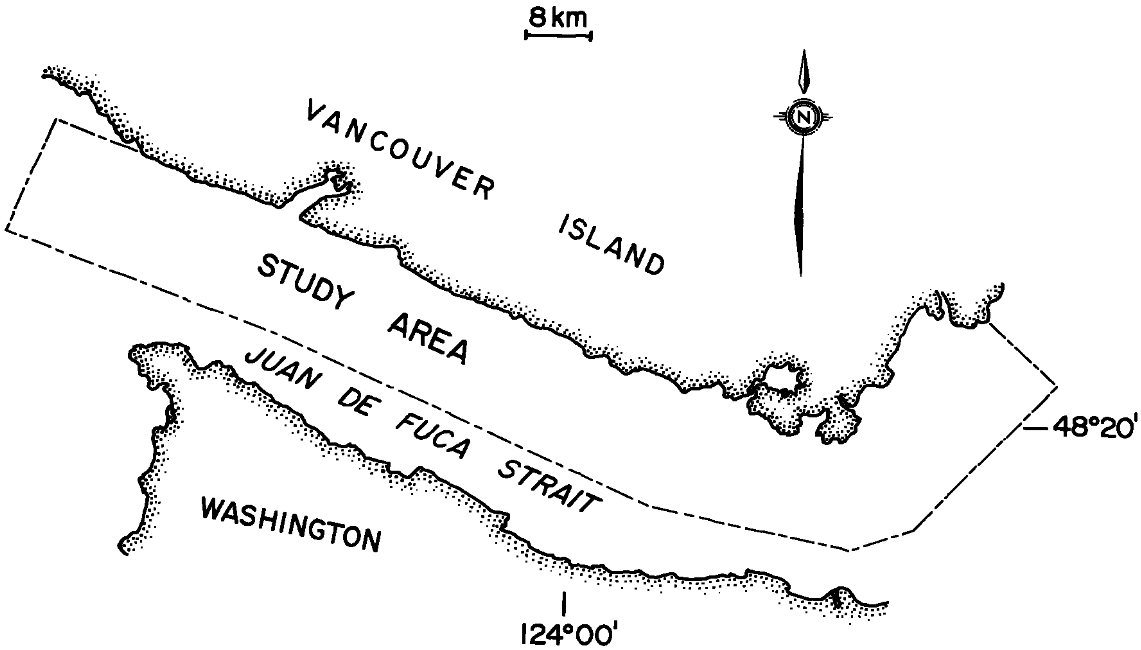

FIGURE 1.—Location of study area in Strait of Juan de Fuca off southwestern Vancouver Island.

Laboratory analysis involved sorting the contents into the classifications outlined in Table 1 by using a low-power binocular microscope. Numbers of organisms in each classification were recorded, if possible, for each individual salmon. Once individuals were counted, displacement volumes (mL) were determined separately for fish contents, for crustacean contents, and for miscellaneous organisms. If organisms were too digested to assign to individual classifications but could be identified as fish or crustaceans, their volumes were included in either the unidentified fish volume or unidentified crustacean volume classification.

Two techniques of data analysis were used.

TABLE 1.—Percentage of salmon sampled with empty stomachs and average number of prey per fish with non-empty stomachs.

Class	N	% empty	Prey type: Sand lance	Herring	Rockfish (*Sebastes*)	Other fish	Euphausiids	*Parathemisto*	Crab larvae	Mysiids	Amphipods*	Crabs	Miscellaneous crustaceans
Sockeye <55 cm	22	46	—	—	—	—	3.7	13.2	5.0	0.3	—	—	0.1
Sockeye >55 cm	117	41	0.2	—	—	—	13.5	8.6	0.4	0.1	—	—	0.4
Total	139	42	0.2	—	—	—	12.1	9.3	1.1	0.1	—	—	0.4
Pink <55 cm	301	26	0.7	—	—	—	9.7	13.7	1.0	0.3	—	0.1	0.3
Pink >55 cm	498	32	0.4	—	—	0.1	15.3	13.1	2.4	0.1	0.1	0.1	0.4
Total	799	30	0.5	—	—	0.1	13.1	13.3	1.9	0.2	0.1	0.1	0.4
Coho <40 cm	1,045	49	0.4	—	—	0.2	6.3	1.2	0.4	1.3	0.1	0.2	0.3
Coho 40-60 cm	1,039	28	5.8	—	0.1	0.3	29.8	0.3	0.9	0.3	—	0.2	0.4
Coho >60 cm	130	32	0.5	0.2	—	—	51.0	0.4	0.6	—	—	—	0.6
Total	2,214	38	3.3	—	—	0.2	22.1	0.7	0.7	0.6	—	0.2	0.4
Chinook <40 cm	607	39	1.1	—	—	0.1	5.4	0.1	0.7	0.4	—	—	0.7
Chinook 40-60 cm	786	36	1.6	0.1	—	0.1	15.3	0.2	0.2	0.6	—	—	0.1
Chinook >60 cm	83	47	0.8	0.3	—	—	62.4	—	0.4	0.1	—	—	—
Total	1,476	38	1.4	0.1	—	0.1	13.6	0.1	0.4	0.5	—	—	0.3

*Other than *Parathemisto*.

Methodology for the first, percent occurrence of each of the prey types, has been outlined by Hynes (1950). All chi-square tests in the analysis for frequency of occurrence of prey types have one degree of freedom. The second technique involved determining percentage by volume of total stomach contents for fish, crustaceans, miscellaneous organisms, and also for the individual prey classifications. Fish, crustaceans, and miscellaneous organisms were recorded by volume, and thus determining percentage of total stomach volume for each classification was direct. For individual prey types, it was necessary to convert numbers of individual organisms to volumes by calculating the volume displaced by a single organism of each prey type. This was done by selecting individual salmon of each species with only one fish and/or one crustacean prey type in the stomach. The unit volumes for each prey type were then calculated as the sum of the fish or crustacean volumes for the selected fish divided by the number of the prey type under consideration. If there was only one unknown in the stomach contents with prey of known (calculated) volumes (the number of prey types multiplied by their unit volumes), the total volume of known prey was subtracted from the total fish or crustacean volume until only one unknown prey class remained. Then the volume of the prey class in question was obtained and its unit volume calculated. Comparisons of prey size among the species were analyzed by analysis of variance.

For an individual salmon with more than one fish or one crustacean prey class in its stomach, volume of each prey class was determined by multiplying the number of organisms by their unit volume. This total volume obtained was scaled proportionately so that individual components when summed equalled the total known fish or crustacean volume.

RESULTS

Volume and Frequency of Food Items

For each species, over 30% of the individuals had empty stomachs (Table 1). In comparing fish with non-empty stomachs, sockeye salmon was the least piscivorous, with a mean 7% fish component in the diet (Fig. 2). In sockeye salmon <55 cm fork length (FL), only 2% of the stomach volume was comprised of fish. At 17% of total food volume, fish was a greater dietary component of pink salmon than of sockeye (Fig. 2). However, the fish component of the diet of sockeye and pink salmon was considerably less than that of coho (46%) and chinook (56%) salmon. Fish comprised 30% of the stomach content volume of coho <40 cm FL, but almost 50% of the stomach content volume of larger coho. Chinook salmon was the most piscivorous of the four species, and the 56% fish component of the diet was constant for the three size classes of chinook salmon investigated, although the species composition of the fish prey changed.

The relative importance of individual prey types was investigated for the four salmon species. Sand lance, *Ammodytes hexapterus*, was virtually the sole fish component of the diet of sockeye salmon, occurring in 4% of the 81 non-empty sockeye salmon stomachs sampled (Fig. 3). Euphausiids were the most important prey for sockeye, occurring in 58% of non-empty stomachs and comprising 71% of the total volume of food eaten. The hyperiid amphipod *Parathemisto* comprised over 11% of the volume of food eaten. Of the fish prey species, sand lance was again the most important for pink salmon, occurring in 9% of 562 non-empty stomachs and comprising 10% of total stomach contents (Fig. 4). There was no significant difference between sockeye and pink salmon in the frequency of occurrence of sand lance in their diets ($\chi^2 = 2.65$, $P > 0.05$). Fish species other than sand lance (herring, *Clupea harengus*, and rockfish, *Sebastes* sp.) comprised less than 1% of stomach contents of pink salmon. As in sockeye salmon, the dominant invertebrate prey types were euphausiids at 62% of stomach content volume and *Parathemisto* at 14%. Frequency of occurrence of euphausiids ($\chi^2 = 1.63$, $P > 0.05$) and *Parathemisto* ($\chi^2 = 3.54$, $P > 0.05$) were similar for sockeye and pink salmon.

Fish species were a significant food for coho and chinook salmon. For example, sand lance occurred in 27% of 1,364 non-empty stomachs of coho salmon, and also comprised 27% of total stomach volume (Fig. 5). Herring comprised <1% of the stomach content volume of coho <40 cm FL, but 25% of the volume for coho >60 cm FL. The dominant invertebrate prey type was euphausiids, comprising 51% of total stomach contents, while all invertebrate prey types combined comprised only 54%. The relative importance of fish as a prey type was greatest in chinook salmon, with sand lance again the dominant prey species, occurring in 34% of 914 non-empty stomachs, and comprising 35% of total volume of contents (Fig. 6). Sand lance occurred in the diet of chinook and coho salmon at similar frequencies ($\chi^2 = 0.80$, $P > 0.05$), as did herring ($\chi^2 = 0.08$, $P > 0.05$). Herring comprised 9% of the stomach contents for chinook salmon <40 cm FL, but 33% of the stomach contents for chinook salmon >60 cm FL.

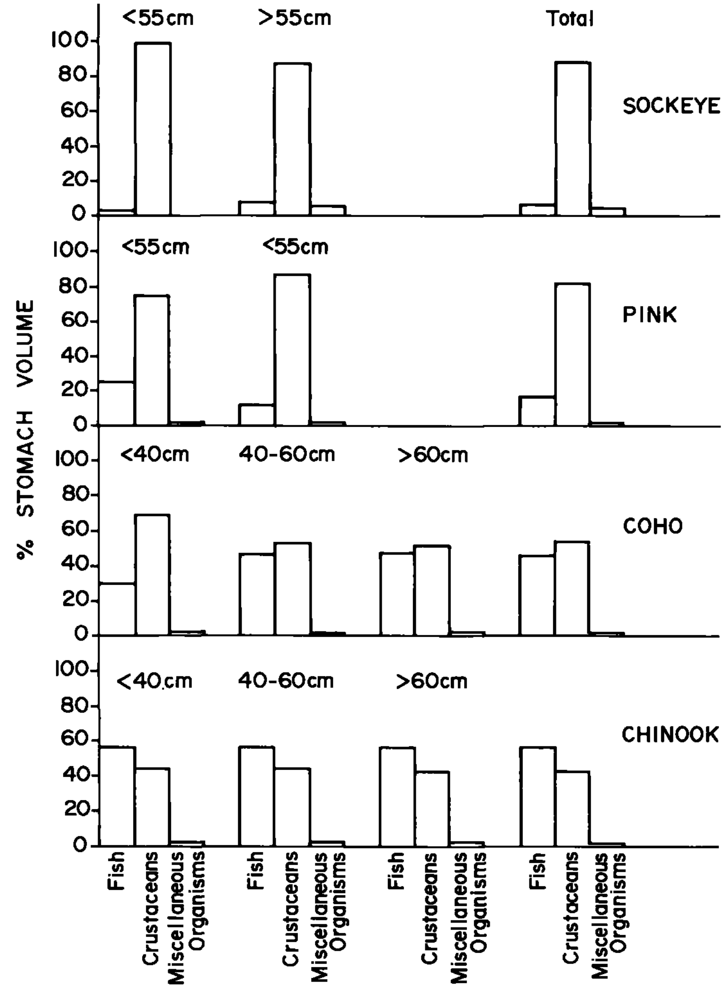

FIGURE 2.—Percentage volumes of stomach contents of the fish, crustacean, and miscellaneous organism component for sockeye, pink, coho, and chinook salmon sampled in Strait of Juan de Fuca during 1967-68.

Coho ate greater numbers of fish than did chinook salmon (Table 1), but chinook had a greater volume of the stomach contents composed of fish (56% chinook, 46% coho). This result suggests chinook eat larger fish than coho (Table 2). As with coho, euphausiids were the dominant invertebrate prey type of chinook salmon, comprising 40% of a total invertebrate volume of 44% of stomach contents. However, euphausiids occurred significantly more often in the diet of coho salmon than in chinook salmon (χ^2 = 4.73, $P < 0.01$).

Fish were a more significant dietary component of chinook and coho salmon than of sockeye and pink salmon. Sand lance occurred significantly more often in the diet of chinook and coho salmon than in the diet of sockeye and pink salmon (χ^2 = 152.9, $P <$ 0.01). Similar results were also found for herring (χ^2 = 18.1, $P < 0.01$), rockfish (χ^2 = 7.2, $P < 0.01$), and mixed fish species (χ^2 = 39.0, $P < 0.01$). Invertebrate prey were more significant in the diet of sockeye and pink salmon than in that of chinook and coho. Euphausiids occurred more frequently in the diet of sockeye and pink salmon (χ^2 = 199.3, $P <$ 0.01), as did *Parathemisto* (χ^2 = 619.5, $P < 0.01$), crab larvae (χ^2 = 171.1, $P < 0.01$), and amphipods (χ^2 = 9.2, $P < 0.01$). There was no difference in frequency of occurrence of crabs in the diet (χ^2 = 0.01, $P > 0.05$) which occurred only at low levels or not at all, but mysiids occurred more frequently in the diet of chinook and coho salmon than in

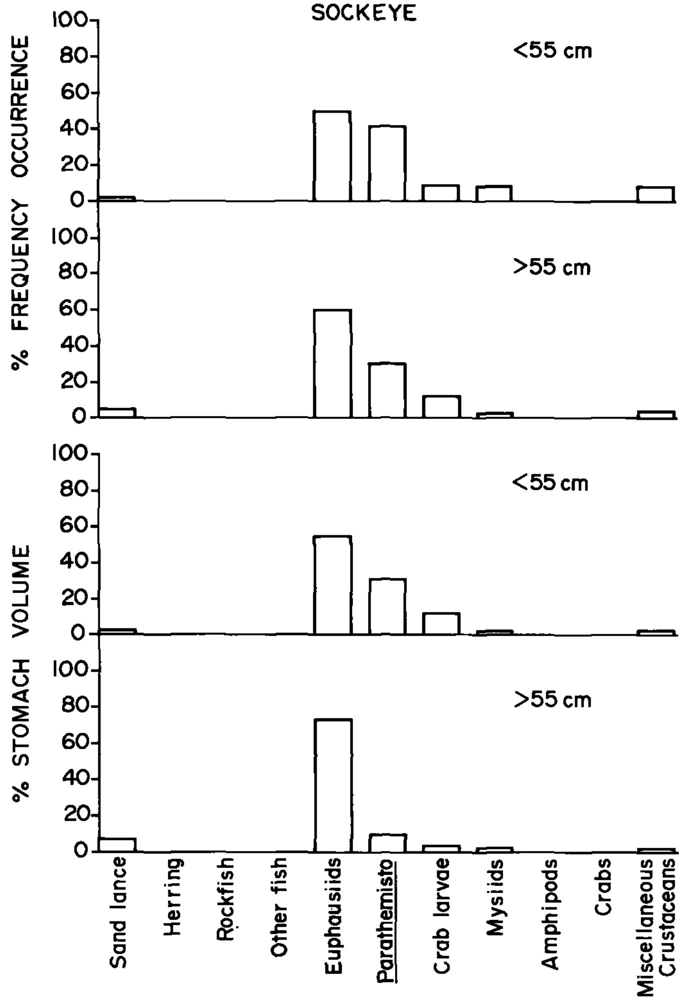

FIGURE 3.—Percentage frequency of occurrence and percentage stomach volume of prey types listed in Table 1 for sockeye salmon.

that of sockeye and pink salmon (χ^2 = 36.0, $P < 0.01$).

Predator and Prey Size

The effect of predator size on the abundance and size of prey was examined for each of the four salmon species investigated. Numbers of individuals consumed for each prey type were tallied for each salmon examined. For the fish prey species, only sand lance was consumed at a high enough frequency to enable one to investigate numbers of sand lance consumed versus predator size. For the four salmon species, there was no consistent trend for sand lance in this regard (Table 1). For both chinook and coho salmon—the two primary sand lance predators—the number of sand lance eaten was greater in the middle size group than in either the small or large size classes. Large chinook and coho salmon switched from sand lance to larger fish species, such as herring (Figs. 5, 6). There were, however, clear trends for some of the invertebrate prey types. The average number of euphausiids eaten per individual predator increased with increasing fish size (Table 1). However, the average number of *Parathemisto* eaten decreased with increasing predator size. The other prey types occurred at a low frequency (Figs. 3-6), and thus it was not possible to determine reliable trends.

As predator size increased, more euphausiids, but

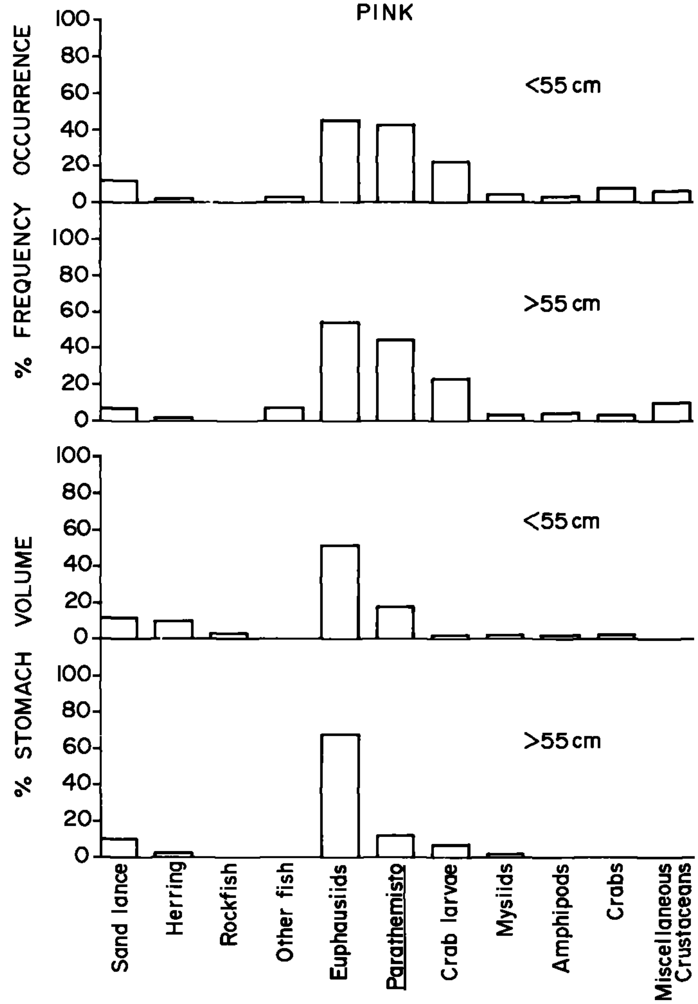

FIGURE 4.—Percentage frequency of occurrence and percentage stomach volume of prey types for pink salmon.

less *Parathemisto*, were eaten per individual predator. The difference in predator response to euphausids and *Parathemisto* may be examined in relation to the size of the prey. The unit volumes of an individual euphausiid were about four times larger than those of an individual *Parathemisto* (Table 2). In each salmon species examined, as the predators increased in size, they switched from the smaller *Parathemisto* to the larger euphausiids and also crab larvae, consuming greater numbers of the larger prey and decreasing numbers of the smaller prey. Chinook and coho salmon also consumed significantly larger *Parathemisto* than did sockeye and pink salmon (F = 4.9; df = 3,98; $P < 0.01$). For the invertebrate prey, an increase in predator size resulted in greater numbers of larger prey being consumed.

As predator size increased, there was an increase in the size of the prey consumed (Table 2). Larger predators consumed larger sand lance and herring. Chinook and coho salmon consumed larger sand lance (F = 3.7; df = 3,613; $P < 0.05$) and mixed fish species (F = 2.9; df = 2,128; $P < 0.05$) than did sockeye and pink salmon. In coho and chinook salmon, there was also a tendency for larger salmon to switch prey types from the smaller sand lance to the larger herring and rockfish. Increasing predator size produced shifts in both the type, number, and size of the prey consumed.

Changes in size of prey and predators were in-

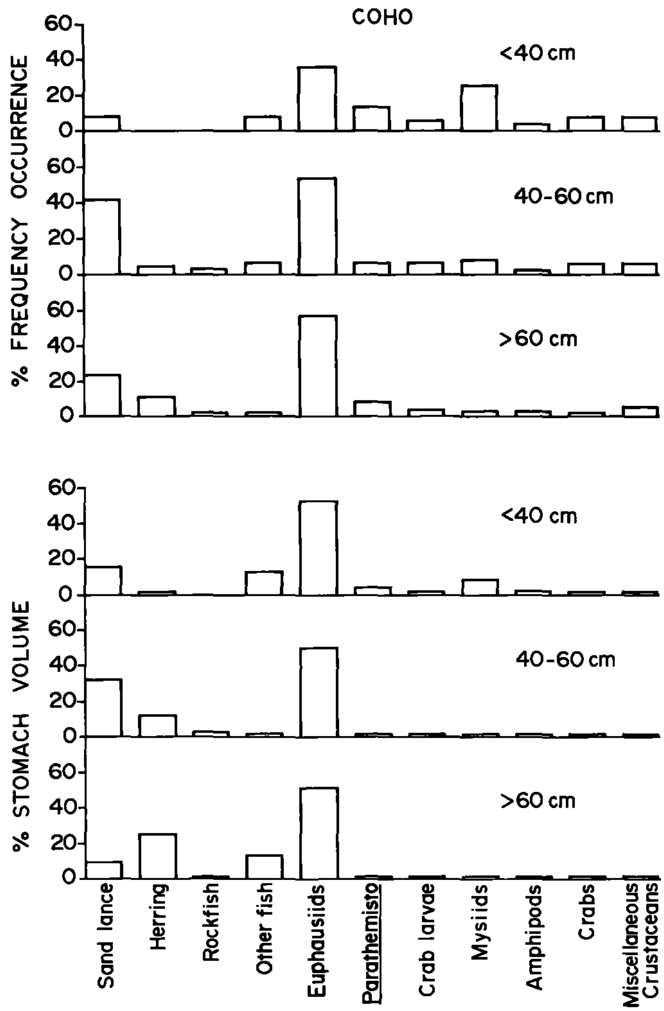

FIGURE 5.—Percentage frequency of occurrence and percentage stomach volume of prey types for coho salmon.

vestigated for the two most frequently occurring fish prey (sand lance, herring) and crustacean prey (euphausiids, *Parathemisto*). Size classes for sockeye and pink salmon were below and above 55 cm FL, and those for chinook and coho salmon below and above 60 cm FL. I assume that the value of the cube root of the volume ratio of the prey is proportional to the prey length ratio, and thus changes in prey size can be compared with changes in predator size.

Mean size of the fish component of the prey increased as predator size increased (Table 3). As the size of pink, coho, and chinook salmon increased by 13%, 65%, and 69%, respectively, the size of the sand lance consumed increased by 16%, 83%, and 83%, respectively. The size of herring eaten also increased as predator size increased, and for pink and chinook salmon it was about equal to the increase in size of the predator species. When the predator responses to increase in size of both prey species are pooled, there is a weak correlation between increasing predator length and increasing prey length ($r = 0.69$, $n = 6$, $P > 0.05$); but if the coho salmon response to increasing herring size is deleted, the relationship is much stronger between increasing predator and prey size ($r = 0.98$, $n = 5$, $P < 0.01$).

Apparent trends of invertebrate prey size with predator size were not statistically significant. For sockeye and pink salmon, mean size of individuals in the two invertebrate prey classes decreased as

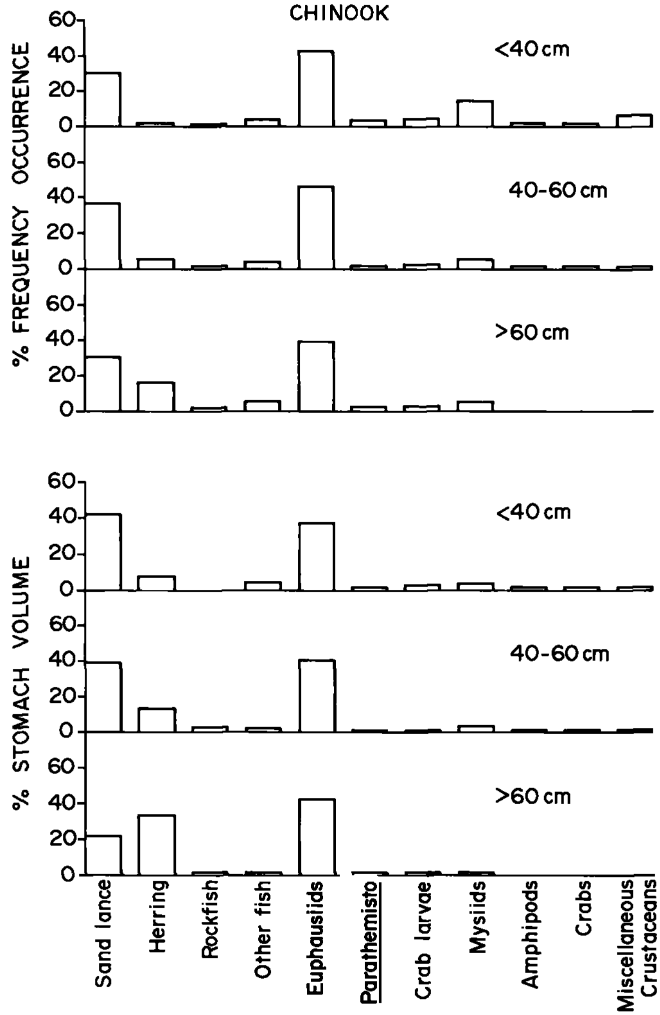

FIGURE 6.—Percentage frequency of occurrence and percentage stomach volume of prey types for chinook salmon.

predator size increased, but not significantly (Table 3) ($r = -0.24$, $n = 4$, $P > 0.05$). For chinook and coho salmon, mean size of the invertebrate prey increased as predator size increased ($r = 0.42$, $n = 4$, $P > 0.05$). However, the increase in prey size was considerably less than the increase in predator size (Table 3).

The results of the previous analyses are summarized as follows. As predator size increased, individual predators selected larger fish prey of one species, but not a greater number of the prey. There was also a shifting from smaller prey species (sand lance) to larger ones (herring, rockfish). As predator size increased, there was a tendency to shift from smaller invertebrate prey (*Parathemisto*) to larger types (euphausiids, crab larvae). Greater numbers of the larger prey were consumed by an individual predator, while numbers of smaller prey consumed declined. Although larger invertebrate prey types were preferred as predator size increased, larger individuals of each prey class were not necessarily selected by larger predators.

Species Comparisons

The dietary components of the four species of salmon investigated are different, and there is more than one possible reason for the apparent partitioning of diet among the salmon species. Perhaps because the salmon occupied different depth zones, the differences in diet are attributable simply to dif-

TABLE 2.—Calculated mean volumes (ml) per individual for prey organisms. These values were used to convert prey numbers to prey volumes. Sample sizes are in parentheses.

Class	Sand lance	Herring	Rockfish (*Sebastes*)	Other fish	Euphausiids	*Parathemisto*	Crab larvae	Mysids	Amphipods	Crabs	Miscellaneous crustaceans
Sockeye											
<55 cm	—	—	—	—	1.24 (4)	0.18 (3)	0.17 (1)	—	—	—	—
>55 cm	3.18 (3)	—	—	—	0.81 (29)	0.13 (8)	1.00 (2)	2.86 (1)	—	—	0.07 (2)
Total	3.18 (3)	—	—	—	0.86 (33)	0.14 (11)	0.72 (3)	2.86 (1)			
Pink											
<55 cm	3.01 (24)	90.00 (4)	26.00 (1)	4.50 (6)	1.17 (85)	0.27 (48)	0.30 (8)	0.93 (4)	1.00 (1)	—	—
>55 cm	4.75 (20)	120.00 (1)	—	1.68 (18)	0.98 (156)	0.57 (68)	0.57 (18)	0.50 (4)	1.17 (1)	0.50 (4)	0.30 (7)
Total	3.80 (44)	96.00 (5)	26.00 (1)	2.39 (24)	1.05 (241)	0.21 (116)	0.49 (26)	0.72 (8)	1.09 (2)	0.50 (4)	0.30 (7)
Coho											
<40 cm	4.33 (38)	32.50 (2)	—	7.36 (40)	1.27 (161)	0.46 (37)	0.35 (13)	1.00 (86)	0.90 (12)	0.71 (18)	0.19 (95)
40-60 cm	4.40 (289)	170.34 (24)	21.32 (9)	3.39 (36)	1.33 (349)	0.42 (20)	0.64 (17)	2.31 (30)	1.43 (7)	0.86 (18)	0.38 (7)
>60 cm	26.98 (19)	207.50 (10)	12.00 (1)	888.00 (1)	1.44 (48)	0.60 (2)	1.00 (2)	2.00 (1)	3.67 (3)	0.33 (1)	1.00 (2)
Total	5.63 (346)	173.00 (36)	20.39 (10)	16.94 (77)	1.32 (558)	0.45 (59)	0.54 (32)	1.34 (117)	1.45 (22)	0.77 (37)	0.22 (104)
Chinook											
<40 cm	6.09 (106)	57.71 (5)	16.00 (1)	10.08 (14)	1.28 (130)	0.20 (2)	0.55 (8)	1.29 (37)	2.14 (5)	0.70 (2)	0.13 (10)
40-60 cm	9.88 (169)	51.56 (22)	37.00 (6)	6.31 (17)	1.14 (190)	0.38 (7)	0.31 (8)	2.11 (21)	2.00 (1)	1.00 (1)	4.11 (3)
>60 cm	51.40 (12)	245.45 (7)	30.00 (1)	1.00 (1)	1.40 (16)	0.55 (1)	0.68 (1)	2.20 (2)	—	—	—
Total	10.22 (287)	92.38 (34)	33.50 (8)	7.79 (32)	1.21 (336)	0.36 (10)	0.44 (17)	1.66 (58)	2.12 (6)	0.80 (3)	1.05 (13)

TABLE 3.—Mean lengths (cm) of salmon and mean size of prey. Mean lengths of sockeye and pink salmon were for those in the size classes below (L_1) and above (L_2) 55 cm, whereas those for coho and chinook salmon were those below (L_1) and above (L_2) 60 cm. The prey ratio $\sqrt[3]{V_2/V_1}$ is assumed to be indicative of ratios in prey lengths between the two groups of predators. The two most frequent fish and invertebrate prey species listed are euphausiids (EU), *Parathemisto* (PA), sand lance (SL), and herring (HR).

Predator				Prey				
Species	Mean length L_1	Mean length L_2	$\frac{L_2}{L_1}$	Prey types	Mean volume V_1	Mean volume V_2	$\frac{V_2}{V_1}$	$\sqrt[3]{\frac{V_2}{V_1}}$
Sockeye	50.7	58.7	1.16	EU	1.24	0.81	0.65	0.87
				PA	0.18	0.13	0.72	0.90
Pink	51.8	58.5	1.13	SL	3.01	4.75	1.58	1.16
				HR	90.00	120.00	1.33	1.10
				EU	1.17	0.98	0.84	0.94
				PA	0.27	0.17	0.62	0.86
Coho	40.0	65.8	1.65	SL	4.39	26.98	6.15	1.83
				HR	159.73	207.50	1.30	1.09
				EU	1.31	1.44	1.10	1.03
				PA	.45	.60	1.33	1.10
Chinook	41.2	69.5	1.69	SL	8.42	51.4	6.10	1.83
				HR	52.70	245.45	4.66	1.67
				EU	1.20	1.40	1.17	1.05
				PA	0.34	0.55	1.61	1.17

ferences in prey abundances by depth. The numbers of salmon caught with non-empty stomachs were tabulated by depth zone of capture (Table 4). Coho salmon were most abundant in water depths of <18 m, whereas sockeye and pink salmon were most abundant between depths of 18 and 36 m, and chinook salmon most abundant in depths >18 m. Coho and chinook salmon have similar diets, but are found at significantly different depths (χ^2 = 714.7, $P < 0.01$). Thus partitioning of the diets among salmon species is not related simply to water depth.

Morphological characters of the salmon species were compared with their food preferences. Chinook and coho salmon have fewer, shorter, and more widely spaced gillrakers than those of sockeye and pink salmon (Table 5). As gillrakers are used to strain food organisms from water passing over the gills (Lagler et al. 1962), I expected salmon species feeding on planktivorous prey to have more gillrakers that are longer and more closely set than those in primarily piscivorous salmon species. Similar arguments could be made for tooth size (Table 5). Partitioning of the diet among the species of salmon investigated is clearly a reflection of morphological differences among the species.

DISCUSSION

The calculation of unit volumes for individual prey classes is an important component of the analysis. Prey types were assumed to be in a similar state of digestion for the different size classes of each species of salmon so that calculated unit volumes would be comparable. Violation of this assumption may account for the inverse predator-prey size relationship found for sockeye and pink salmon with euphausiids and *Parathemisto*. The analysis of relative sizes of the species eaten assumes that different prey types were not more or less digested than others. This is unlikely to be strictly true, but it was assumed that differential digestability of the prey species did not significantly alter their relative sizes.

Previous work on diet description of *Oncorhynchus* species has indicated that there can be considerable variability in dietary components of a particular species. However, some general conclusions can be drawn. Sockeye salmon are the least piscivorous of the northeast Pacific *Oncorhynchus* species (Allen and Aron 1958; LeBrasseur 1966; Foerster 1968). Euphausiids have been reported consistently as a major contributor to the diet of pink salmon (Maēda 1954; Ito 1964; Takagi et al. 1981). The fish component reported has been variable, ranging from <1% to over 90% of stomach volume (Takagi et al. 1981). Chinook and coho salmon tend to be the most piscivorous (Allen and Aron 1958; Prakash 1962; Reimers 1964; LeBrasseur 1966; Machidori 1972). For chinook salmon, fish were reported to provide

TABLE 4.—Number of salmon caught with non-empty stomachs and depth of water (m) in Strait of Juan de Fuca, British Columbia. Salmon were caught by troll gear. Numbers in parentheses are percent of each species caught in each depth zone.

Depth (m)	Sockeye	Pink	Coho	Chinook
<9.1	8 (9.9)	41 (7.3)	385 (28.1)	20 (2.2)
9.1-18.3	10 (12.3)	95 (16.9)	360 (26.3)	60 (6.6)
18.3-27.4	26 (32.1)	159 (28.3)	269 (19.6)	134 (14.6)
27.4-36.6	23 (28.4)	151 (26.9)	211 (15.4)	267 (29.1)
36.6-45.7	7 (8.6)	65 (11.6)	86 (6.3)	119 (13.0)
45.7-54.8	7 (8.6)	50 (8.9)	58 (4.2)	316 (34.5)
Total	81	561	1,369	916

TABLE 5.—Comparisons of morphometric and meristic characters of Pacific salmon whose dietary components were investigated in this study.

Species	Gillraker No.[1]	Gillraker Spacing[2]	Gillraker Length[3]	Tooth size[4]
Sockeye	33.7	close	2.6	smallest
Pink	30.4	moderate	3.4	small
Coho	21.2	wide	2.1	moderate
Chinook	20.7	wide	2.0	large

[1]From Hikita (1962).
[2]From Morrow (1980).
[3]Gillraker length as percent of postorbital-hypural length. Gillraker length is from Hikita (1962), postorbital-hypural length from Beacham and Murray (1983).
[4]From Vladykov (1962), Hikita (1962).

a larger proportion of the diet of larger chinook salmon than of smaller ones (Milne 1955; Reid 1961). In my study, the fish component of the diet was similar for all size classes of chinook salmon. This may be due to differences in availability of invertebrate prey to the smaller chinook salmon among the studies. For example, Ito (1964) found that squid were the largest dietary component of chinook and coho salmon caught in drift nets in high seas fisheries. Variability in diets of the different species may be due in part to prey abundance, selection by the predator, and possible selectivity by the sampling gear used. Hook and line sampling may select fish of different diets than would perhaps gill nets. Salmon caught by trolling may have a higher component of fish in the diet than those caught by gill nets. In my study, fish did constitute a larger proportion of the diet in larger coho salmon than in smaller ones, as noted for chinook salmon. My study has examined the distribution of prey types and sizes for salmon caught from June to October only. Although the relative proportions of fish and invertebrate prey could change seasonally for the salmon species examined, the relative ranking of the species in terms of proportion of fish in their diet should remain constant.

Availability of prey types can alter markedly the proportions in a predator's diet. Herring comprised over 70% of the stomach contents of troll-caught chinook and coho salmon caught off the east and west coasts of Vancouver Island in 1957 (Prakash 1962). My study showed that during 1967-68, herring comprised <20% of the stomach contents of chinook and coho salmon in the same area. Stock abundances of herring declined rapidly in the late 1960's in British Columbia (Hourston 1978), indicating that during a period of low herring abundance, sand lance became an important dietary component of chinook and coho salmon in this area.

Pink salmon in southern British Columbia and Washington State show 2-yr cycles of abundance, with returns absent in even-numbered years. This pattern of abundance has been suggested to be a result of predation by returning adults of the dominant brood year on fry of the alternate brood year (Ricker 1962). In my study, fish other than sand lance, herring, or rockfish comprised <1% of the stomach contents of pink salmon sampled in 1967. These results suggest that predation by the dominant broodline on the alternate broodline may be neither necessary nor sufficient to account for cycles in pink salmon abundance.

The effect of prey size on selection by planktivorous fish has been examined by Werner and Hall (1974), O'Brien et al. (1976), O'Brien (1979), Gibson (1980), and Eggers (1982). Eggers found that juvenile sockeye salmon prefer large nonevasive prey, but will eat small and/or evasive prey when the former is not available. I found that as predator size increased, prey size increased also, both in terms of size of individuals within a prey type, and a shifting from smaller to larger prey types. The predators presumably decrease the amount of time and energy needed to ingest a given amount of food by switching from smaller to larger prey, given that the large prey types are sufficiently abundant. Werner and Hall (1974) attributed a preference by predators for only a part of the prey types available as a method for increasing foraging efficiency. These results suggest that the salmon species examined do select prey both for size and availability, presumably to increase foraging efficiency.

Morphological differences and diet partitioning have been previously noted for many fish species (Keast and Webb 1966; Hyatt 1979). As outlined by Hyatt (1979), many planktivorous feeding fish tend to have numerous, well-developed, close-set gillrakers. My study indicated that the more piscivorous chinook and coho salmon have fewer gillrakers than the more planktivorous sockeye and pink salmon. Lake trout, *Salvelinus namaycush*, populations that are more planktivorous also have more and longer gillrakers than less planktivorous ones (Martin and Sandercock 1967). *Oncorhynchus masou* (masou or cherry salmon), found in the western Pacific Ocean, has fewer gillrakers than either chinook or coho salmon (Hikita 1962) and, as an adult, feeds largely on fish (Tanaka 1965). Chum, *O. keta*, salmon have an average of 2-3 more gillrakers than chinook and coho (Hikita 1962), and the diet of chum salmon sampled in the spring and summer during 1956-63 in the North Pacific comprised between 10 and 35% fish (Neave et al. 1976). In the genus *Oncorhynchus*, as gillraker number declines, the proportion of fish in the diet increases. Morphological differences among the species account for a greater partitioning of the diet than do differences in water depths in which the individual species are located.

Pacific salmon are adaptable in their diet, shifting their preferred prey species in relation to prey size and abundance. It seems unlikely that salmon abundance is affected by the abundance of any one type of prey. For example, the decline in abundance of British Columbia herring stocks was not followed immediately by declines in salmon abundance. Growth rates of salmon may be affected by changes in diet and this could have an impact on stock population dynamics.

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LITERATURE CITED

ALLEN, G. H., AND W. ARON.
1958. Food of the salmonid fishes of the western North Pacific Ocean. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 237, 11 p.

BEACHAM, T. D., AND C. B. MURRAY.
1983. Sexual dimorphism in the adipose fin of Pacific salmon (*Oncorhynchus*). Can. J. Fish. Aquat. Sci. 40:2019-2024.

EGGERS, D. M.
1982. Planktivore preference by prey size. Ecology 63:381-390.

FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162:1-422.

FRENCH, R., H. BILTON, M. OSAKO, AND A. HARTT.
1976. Distribution and origin of sockeye salmon (*Oncorhynchus nerka*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 34, 113 p.

GIBSON, R. M.
1980. Optimal prey-size selection by three-spine sticklebacks (*Gasterosteus aculeatus*): a test of the apparent-size hypothesis. Z. Tierpsychol. 52:291-307.

GODFREY, H., K. A. HENRY, AND S. MACHIDORI.
1975. Distribution and abundance of coho salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 31, 80 p.

GRAHAM, C. C., AND A. W. ARGUE.
1972. Basic data on Pacific salmon stomach contents and effort for 1967 and 1968 test trolling catches in Juan de Fuca Strait, British Columbia. Can. Dep. Environ. Fish. Serv., MS Rep. 1972-76, 405 p.

HIKITA, T.
1962. Ecological and morphological studies of the genus *Oncorhynchus* (Salmonidae) with particular consideration on phylogeny. Sci. Rep. Hokkaido Salmon Hatchery 17, 60 p.

HOURSTON, A. S.
1978. The decline and recovery of Canada's Pacific herring stocks. Can. Fish. Mar. Serv. Tech. Rep. 784, 17 p.

HYATT, K. D.
1979. Feeding Strategy. *In* W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. VIII, Bioenergetics and growth, p. 71-119. Acad. Press, N.Y.

HYNES, H. B. N.
1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of the methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

ITO, J.
1964. Food and feeding habits of Pacific salmon (genus *Oncorhynchus*) in their oceanic life. Hokkaido Reg. Fish. Res. Lab. Bull. 29:85-97. (Engl. transl., Fish. Res. Board Can. Transl. Ser., 1309.)

KEAST, A., AND D. WEBB.
1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23:1845-1874.

LAGLER, K. F., J. E. BARDACH, AND R. R. MILLER.
1962. Ichthyology. John Wiley and Sons, Inc., N.Y., 545 p.

LEBRASSEUR, R. J.
1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23: 85-100.

MACHIDORI, S.
1972. Observations on latitudinal distribution of offshore coho salmon in early summer, with reference to water temperature and food organisms. Jpn. Far Seas Fish. Res. Lab. Bull. 6, p. 101-110.

MAĒDA, H.
1954. Ecological analyses of pelagic shoals—I. Analysis of salmon gill-net association in the Aleutians. (1) Quantitative analysis of food. Jpn. J. Ichthyol. 3:223-231.

MAJOR, R. L., J. ITO, S. ITO, AND H. GODFREY.
1978. Distribution and origin of chinook salmon (*Oncorhynchus tshawytscha*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 38, 54 p.

MARTIN, N. V., AND F. K. SANDERCOCK.
1967. Pyloric caeca and gill raker development in lake trout, *Salvelinus namaycush*, in Algonquin park, Ontario. J. Fish. Res. Board Can. 24:965-974.

MILNE, D. J.
1955. Selectivity of trolling lures. Fish. Res. Board Can. Prog. Rep. Pac. Coast Stn. 103:3-5.

MORROW, J. E.
1980. The freshwater fishes of Alaska. Alaska Northwest Publ. Co., Anchorage, AK, 248 p.

NEAVE, F., T. YONEMORI, AND R. G. BAKKALA.
1976. Distribution and origin of chum salmon in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 35, 79 p.

O'BRIEN, W. J.
1979. The predator-prey interaction of planktivorous fish and zooplankton. Am. Sci. 67:572-581.

O'BRIEN, W. J., N. A. SLADE, AND G. L. VINYARD.
1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57:1304-1310.

PARKER, R. R.
1971. Size selective predation among juvenile salmonid fishes in a British Columbia inlet. J. Fish. Res. Board Can. 28: 1503-1510.

PRAKASH, A.
1962. Seasonal changes in feeding of coho and chinook (spring) salmon in southern British Columbia waters. J. Fish. Res. Board Can. 19:851-866.

REID, G. M.
1961. Stomach content analysis of troll-caught king and coho salmon, Southeastern Alaska, 1957-58. U.S. Fish Wildl. Serv., Spec. Sci. Rep. 379, 8 p.

REIMERS, P. E.
1964. A modified method of analyzing stomach contents with notes on the food habits of coho salmon in the coastal waters of Oregon and southern Washington. Fish. Comm. Oreg. Res. Briefs 10, p. 46-56.

RICKER, W. E.
1962. Regulation of the abundance of pink salmon populations.

In N. J. Wilimovsky (editor), Symposium on Pink Salmon, p. 155-211. Inst. Fish., Univ. Br. Columbia, Vancouver, B.C.

TAKAGI, K., K. V. ARO, A. C. HARTT, AND M. B. DELL.
1981. Distribution and origin of pink salmon (*Oncorhynchus gorbuscha*) in offshore waters of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 40, 195 p.

TANAKA, S.
1965. A review of the biological information on masu salmon (*Oncorhynchus masou*). Int. North Pac. Fish. Comm. Bull. 16, p. 75-135.

VLADYKOV, V. D.
1962. Osteological studies of Pacific salmon of the genus *Oncorhynchus*. Bull. Fish. Res. Board Can. 136, 172 p.

WERNER, E. E., AND D. J. HALL.
1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042-1052.