FOOD AND GROWTH PARAMETERS OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN CENTRAL COLUMBIA RIVER[1]

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ABSTRACT

Juvenile chinook salmon, *Oncorhynchus tshawytscha*, in the Hanford area of the free-flowing central Columbia River, Wash., consume almost entirely adult and larval stages of aquatic insects. Their diet is dominated by midges (Diptera: Chironomidae). By numbers, adult midges provided 64 and 58% of the diet and larval midges 17 and 18% of the diet, in 1968 and 1969, respectively. The families Hydropsychidae (Trichoptera or caddisflies), Notonectidae (Hemiptera or true bugs), and Hypogastruridae (Collembola or springtails) are of minor numerical importance with a combined utilization of 7% in 1968 and 15% in 1969.

Distinctive features of food and feeding activity of juvenile chinook salmon at Hanford are fourfold: 1) the fish utilize relatively few insect groups, predominantly Chironomidae; 2) they depend largely upon autochthonous river organisms; 3) they select prey drifting, floating, or swimming in the water; and 4) they are apparently habitat opportunists to a large extent. Analyses were made of variations in diet and numbers of insects consumed between six sampling stations distributed along a 38-km section of the river. Data are provided on feeding intensity, fish lengths, length-weight relationships, and coefficients of condition. Seasonal changes in river temperature and discharge, as well as variations in regulated flow levels, are environmental features influencing feeding, growth, and emigration of fish in the Hanford environs.

Food habits of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), have been reported from various habitats including the Sacramento River, Calif. (Rutter, 1904); lower Sacramento-San Joaquin system, Calif. (Sasaki, 1966); lower Chehalis River and upper Grays Harbor system, Wash. (Herrmann, 1970); middle Willamette River, Oreg. (Breuser, 1954); and tributaries of the central Columbia River, Wash. (Chapman and Quistorff, 1938). Initial observations on feeding bionomics of juvenile chinook salmon in the central Columbia River were conducted in 1968 (Becker, 1970a). The study was expanded in 1969. The objectives of this report are to present data based on the more extensive 1969 investigation and to discuss theoretically the influence of environmental features.

The mainstem Columbia River above Bonneville Dam has been altered during recent decades into a nearly consecutive series of artificial impoundments arising from hydroelectric development. Only one section of the main channel now survives in its natural, free-flowing condition. This section extends from Richland, Wash., some 93 km upriver to Priest Rapids Dam, where it forms the northern and northeastern boundaries of the Atomic Energy Commission's Hanford Reservation (Figure 1).

Most spawning grounds for salmonids throughout the mainstem Columbia River have now been inundated by the reservoir complex (Fulton, 1968). Maintenance of salmonid resources is due largely to providing access over otherwise impassable dams, propagating young fish in hatcheries and spawning channels,

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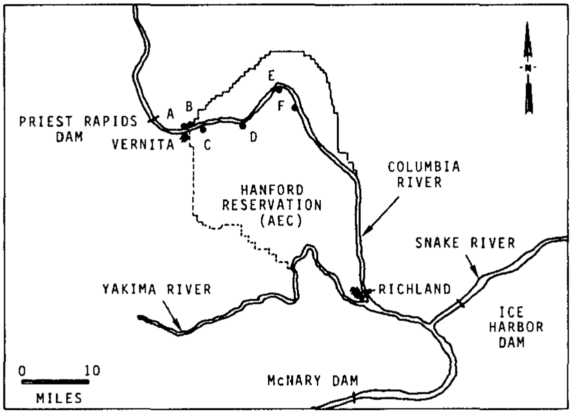

FIGURE 1.—The Hanford environs of the free-flowing Columbia River between Richland, Wash., and Priest Rapids Dam.

and protecting spawning and rearing areas in available tributaries. The free-flowing Hanford section, however, still supports a sizable spawning population of fall chinook salmon that has produced an increase from about 300 redds in 1960 to about 4,500 redds in 1969 (Watson, 1970). The annual contribution of seaward migrants from the Hanford population to the combined natural production of the Columbia and Snake Rivers is not known. But the Hanford population has clearly acquired considerable importance in sustaining natural salmonid runs within the Columbia River Basin.

ENVIRONMENTAL CONDITIONS

River temperatures and discharges are two factors potentially influencing the availability of food organisms, feeding activity, and growth of juvenile chinook salmon in the central Columbia River. The ecological aspects of these two factors are evaluated in the Discussion of this report.

The annual cycles of temperature and discharge (Figure 2) are essentially similar from year to year. Temperatures are lowest in January and February when eggs of fall chinook salmon are buried in the gravel, rise during the spring as fry emerge, and peak during August and September. From the standpoint of known thermal requirements (Brett, 1952), temperatures are well below the thermal preferendum of juvenile chinook salmon (12°-14°C) in March and April, enter the preferred range in May and June—when conditions are presumably optimum for feeding and growth, and extend into the upper zone of thermal tolerance during July and August.

Temperatures at Priest Rapids Dam (above Hanford) were somewhat lower than those

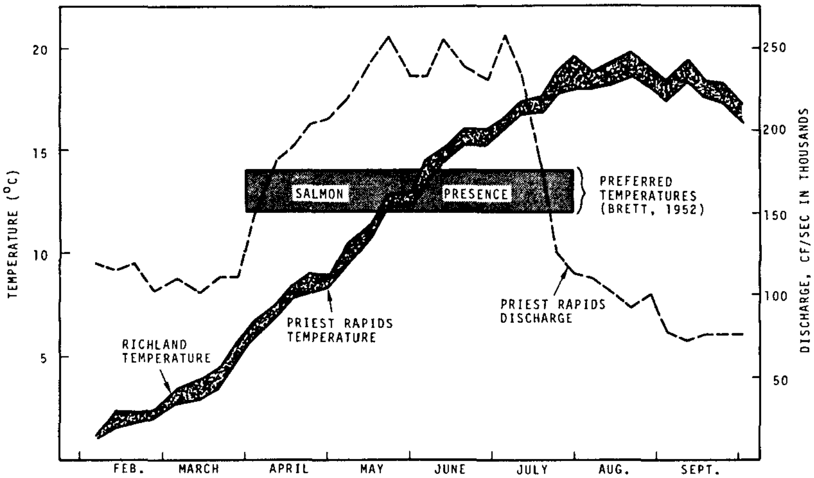

FIGURE 2.—Temperature and flow conditions in the central Columbia River during the spring and summer of 1969, in relation to the presence and preferred temperatures of juvenile fall chinook salmon.

at Richland (below Hanford) in 1969 largely because of thermal discharges from operating plutonium-production reactors on the Hanford reservation.[3] Solar radiation also contributes heat to the free-flowing river above Richland during the summer (Moore, 1968). Maximum daily temperatures recorded in 1969 at Priest Rapids Dam and Richland were 19.7° and 20.6°C, respectively. These peaks were well below the apparent upper incipient lethal level of 25.1°C for juvenile chinook salmon, experimentally determined (Brett, 1952).

The annual volume of river flow in the central Columbia River ranges from about 40,000 to over 300,000 cfs (1,133-8,500 m³/sec). Flows are low during the fall and winter, but increase and peak during April, May, and June due to the seasonal runoff of the spring freshet. In 1969, flows increased about 6 weeks earlier than normal because of operational releases at Grand Coulee Dam on the upper Columbia River. High flows were sustained for about 3 mo, then decreased sharply in July, and minimum summer flows occurred in late August and September.

The discharge data illustrated in Figure 2 are based on weekly means and fail to reveal the extent of either weekly or daily fluctuations in river levels that occur from flow regulation at Priest Rapids Dam. Flows are generally reduced on weekends and increased during the week in response to consumer demands for hydroelectric power (Figure 3). Similar but less extreme variations are induced daily. Water in excess of reservoir capacity is discharged over spillways at Priest Rapids Dam during the spring spate. Weekly fluctuations in river volumes are more variable at other seasons because greater need exists to conserve reservoir water supplies for hydroelectric production. At these times, such as in March and August 1969, flow regulation on weekends may result in changes of water level in the Hanford area of up to 2 m in 24 hr.

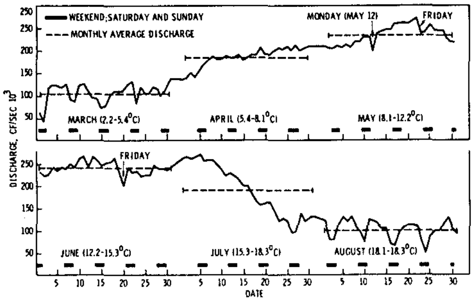

FIGURE 3.—Weekly and daily fluctuations in flow volumes in the central Columbia River due to regulation at Priest Rapids Dam, above Hanford, March-August 1969.

Juvenile fall chinook salmon occur in the Hanford area of the Columbia River from late March to mid-July (Figure 2) (Mains and Smith, 1964; Becker, 1970b). During this span the eggs hatch, fry leave the gravel of the riverbed, and juvenile fish occupy inshore feeding areas for indeterminate periods of feeding and growth before departing seaward. Most juveniles lingering at Hanford emigrate by the end of July. The short residence span is a historical characteristic of juvenile fall chinook salmon originating in the central Columbia River. However, the timing of the seaward migration of juvenile salmonids passing through the upper and lower Columbia River system is now delayed by the reservoir complex (Park, 1969; Raymond, 1969).

METHODS

Juvenile chinook salmon of the 0-age group, produced by adults spawning during the fall of 1968, were collected by seines at stations along the river banks from 4 March to 29 July 1969. The sampling span corresponded to the annual presence of fish following emergence from the gravel and preceding seaward migration. Stomach analyses of 769 fish were made from samples collected at roughly weekly intervals, when available. All samples were collected between 0900 and 1500 hr, and preserved in 10% buffered Formalin[4] immediately

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[3] Four reactors were discharging heated water in 1968 and the spring of 1969. The effluents issued as point discharges from subsurface locations in midriver at depths exceeding 6 m, and the mixing zones extended downstream in narrow bands prior to dispersal. Juvenile salmonids feeding in inshore areas below the reactors were not directly exposed to thermal increments.

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

after capture to stop digestive action. The fish were later measured (fork length, FL) and eviscerated. All measurements were taken after 7 days of preservation to obtain consistency, since Formalin causes some initial shrinkage. Organisms in the stomachs were identified individually to the lowest practical category under a dissecting microscope with the aid of appropriate taxonomic texts, classified according to their developmental stage, and enumerated. Insects represented by chitinous head capsules, particularly larval Chironomidae, were counted as complete organisms whereas fragmented body parts were excluded.

The 1968 study quantified only the food organisms consumed. Methods in 1969 were modified to provide data on fish length-weight relationships and dry weight (biomass) of the stomach contents. Fish were individually blotted with absorbent paper to remove excess fluid prior to weighing. After identification and enumeration of food organisms, the entire stomach content of each fish was placed in a miniature watch glass, air dried at least 24 hr in a controlled atmosphere, and weighed.

Collecting stations were distributed along a 38-km section of the Columbia River extending downstream from the Highway 240 bridge at Vernita, Wash. Six primary stations, shown in Figure 1 (A, B, C, D, E, F), and four supplementary stations were used. Samples from all 10 stations were combined in summations of food organisms utilized (see Tables 1 and 2), but only data from the six primary stations were used for subsequent statistical treatment.

RESULTS

Food Organisms Utilized

Throughout their sojourn at Hanford, over 95% of the diet of juvenile chinook salmon consisted of insects. The prey included adult, subadult, and larval stages of semiaquatics, various developmental stages of aquatics, and winged adults of terrestrials (Table 1). Comparison of the 1968 and 1969 data in Table 1 reveals that the organisms consumed were essentially similar in two successive years.

The Chironomidae (midges) were the dominant insect group utilized. Emerging subadults and adults were captured in abundance, 64% in 1968 and 58% in 1969. Midge larvae were taken less extensively, 17% in 1968 and 18% in 1969. Few midge pupae and no pupal exuviae were noted.

The order Diptera provided 83% and 78% of all insects utilized in 1968 and 1969, respectively. Other insect groups were of less importance in terms of numbers, but not necessarily in volume (or nutritional value) since sizes of different species vary considerably. The relatively large Trichoptera (caddisflies), consisting primarily of *Hydropsyche cockerelli* (Hydropsychidae), were numerically the second most important order. Like the midges, most caddisflies eaten were recently emerged adults associated with the water-air interface. Other groups of secondary importance were the families Notonectidae (Hemiptera or true bugs), primarily small *Notonecta* nymphs, and the Hypogastruridae (Collembola or springtails).

Few Ephemeroptera (mayflies), often important dietary items of salmonids in other streams, and no Plecoptera (stoneflies) were detected in the stomach contents. Unpublished data from limited bottom samples, sporadic drift samples, inspection of stones, and trapping of adult insects by light attraction at night indicate that populations of mayflies and particularly stoneflies are low in the central Columbia River. Zooplankton, originating primarily from the Priest Rapids reservoir and present in the river drift, were utilized in small quantities by only a few fish.

Seasonal Changes in Diet

Some change occurs in the diet of juvenile chinook salmon from March to July (Table 2). The Chironomidae accounted for the greatest proportion of food organisms each month on a numerical basis, with the most larval and adult midges being consumed in March and April. Hemiptera and Collembola, both consisting of small forms, received maximum utilization in April, May, and June when rising river volumes inundated shoreline areas. Adult Trichoptera were consumed primarily in June

TABLE 1.—Organisms consumed by juvenile chinook salmon (0-age group) in the central Columbia River. (435 fish examined in 1968 and 769 fish in 1969.)

	1968[1]		1969	
Food organism	Number	%	Number	%
Diptera:				
Adults:				
Chironomidae[2]	5,973	63.5	11,062	58.2
Dolichopodidae	31	0.3	6	[3]0.0
Empididae	13	0.1	4	0.0
Simuliidae	4	0.0	52	0.3
Culicidae	0	—	6	0.0
Ephydridae	1	0.0	3	0.0
Heleidae	0	—	1	0.0
Stratiomyidae	0	—	1	0.0
Dixidae	0	—	1	0.0
Unidentified	82	0.9	193	1.0
Larvae:				
Chironomidae	1,596	17.0	3,450	18.1
Dolichopodidae	18	0.2	4	0.0
Empididae	0	—	1	0.0
Simuliidae	55	0.6	54	0.3
Ephydridae	1	0.0	1	0.0
Heleidae	3	0.0	0	—
Muscidae	3	0.0	0	—
Unidentified	7	0.1	9	0.0
Pupae:				
Chironomidae	7	0.1	18	0.1
Tipulidae	5	0.1	0	—
Heleidae	0	—	2	0.0
Unidentified	5	0.1	4	0.0
Total Diptera	7,804	83.0	14,872	78.3
Hemiptera:				
Notonectidae	248	2.6	918	4.8
Mesoveliidae	34	0.4	2	0.0
Macroveliidae	1	0.0	0	—
Corixidae	1	0.0	1	0.0
Saldidae	4	0.0	8	0.0
Hebridae	1	0.0	0	—
Unidentified	11	0.1	27	0.1
Total Hemiptera	300	3.2	956	5.0
Coleoptera:				
Adults:				
Unidentified	4	0.0	23	0.1
Larvae:				
Dytiscidae	26	0.3	13	0.1
Noteridae	1	0.0	0	—
Hydrophilidae	1	0.0	1	0.0
Elmidae	0	—	1	0.0
Ptilodactylidae	1	0.0	0	—
Unidentified	1	0.0	16	0.1
Total Coleoptera	34	0.4	54	0.3
Lepidoptera:				
Unidentified adults[4]	3	0.0	187	1.0
Unidentified larvae[4]	0	—	21	0.1
Total Lepidoptera	3	0.0	208	1.1
Trichoptera:				
Adults:				
Hydropsychidae	277	2.9	948	5.0
Psychomyiidae	0	—	3	0.0
Calamoceratidae	0	—	6	0.0
Hydroptilidae	0	—	12	0.1
Unidentified	93	1.0	44	0.2
Larvae:				
Hydropsychidae	18	0.2	93	0.5
Psychomiidae	13	0.1	5	0.0
Phryganeidae	1	0.0	0	—
Rhyacophilidae	0	—	2	0.0
Unidentified	13	0.1	27	0.1
Total Trichoptera	415	4.4	1,140	6.0
Ephemeroptera:				
Subimagos:				
Unidentified	8	0.1	0	—
Nymphs:				
Baetidae	1	0.0	24	0.1
Unidentified	0	—	4	0.0
Total Ephemeroptera	9	0.1	28	0.1
Hymenoptera:				
Unidentified adults	26	0.3	27	0.1
Homoptera:				
Adults:				
Aphididae	49	0.5	245	1.3
Aleyrodidae	1	0.0	0	—
Unidentified	40	0.5	28	0.1
Total Homoptera	90	1.0	273	1.4
Collembola:				
Hypogastruridae	115	1.2	974	5.1
Other insects:				
Thysanoptera	35	0.4	11	0.1
Megaloptera	1	0.0	1	0.0
Unidentified adults	0	—	98	0.5
Unidentified larvae	0	—	11	0.1
Unidentified	165	1.7	51	0.3
Total other insects	201	2.1	172	0.9
Total insects	8,997	95.7	18,704	98.4
Other food items:				
Fish larvae	0	—	18	0.1
Acari	276	2.9	169	0.9
Zooplankton	[5] 30	0.3	[5] 15	0.1
Algae	[6] 1	0.0	0	—
Arachnida	93	1.0	97	0.5
Plant seeds	5	0.1	1	0.0
Total other food items	405	4.3	300	1.6

[1] 1968 data from Becker (1970a).
[2] Primarily emerging subadults.
[3] Less than 0.05%.
[4] Primarily *Parargyractic* sp. (Pyralidae).
[5] Number of fish containing small quantities of Cladocera, Ostracoda, Copepoda, or Amphipoda.
[6] A quantity of *Anacystis*.

TABLE 2.—Monthly changes in diet of juvenile chinook salmon in 1969, all sampling stations combined.

Food organism	Consumption per month (%)				
	March	April	May	June	July
Diptera[1]	99.5	88.8	70.2	77.2	84.8
Chironomidae, adults	67.1	62.4	50.4	52.4	77.2
Chironomidae, larvae	31.8	24.6	17.4	22.8	6.3
Hemiptera[1]	—	3.2	13.2	2.6	T[2]
Coleoptera	T	T	T	T	T
Lepidoptera	—	T	T	3.3	T
Trichoptera[1]	—	T	T	10.2	13.0
Ephemeroptera	—	T	—	T	T
Homoptera	—		T	3.4	T
Hymenoptera	—	T	T	T	T
Collembola[1]	T	5.6	13.8	1.4	—
Unknowns	—	—	T	T	—
All other insects	—	T	T	1.3	T
Total insects	99.5	97.6	97.2	99.4	97.8

[1] Major insect groups utilized.
[2] "T" = "Trace," less than 1% by number in stomach contents.

and July, in association with summer emergence of the univoltine caddisfly populations. A minor group, the semiaquatic Pyralidae (Lepidoptera or moths and butterflies), were taken most heavily in June.

Some correlation of diet (Table 2) with fish size (Figure 4) was evident. Chinook salmon fry were relatively small (35-40 mm FL) and had incompletely absorbed yolk sacs when they emerged from the gravel and began feeding in March and April. Food organisms selected by fry were predominantly small forms, primarily midges but some *Notonecta* nymphs and Collembola were included. Adult Trichoptera in June and July were selected primarily by large fish (>50 mm FL) capable of capturing and swallowing these larger insects.

Use of Drift Organisms

The developmental stages of insects ingested by juvenile chinook salmon reveal that most were floating, drifting, or swimming in the water when captured. This was apparently the situation for the selection of most Chironomidae, Hydropsychidae, *Notonecta* nymphs, and Hypogastruridae, the four main insect forms utilized. Relatively few insect stages normally adhering to epibenthic substrates or living within gravel interstices were represented in the stomach contents.

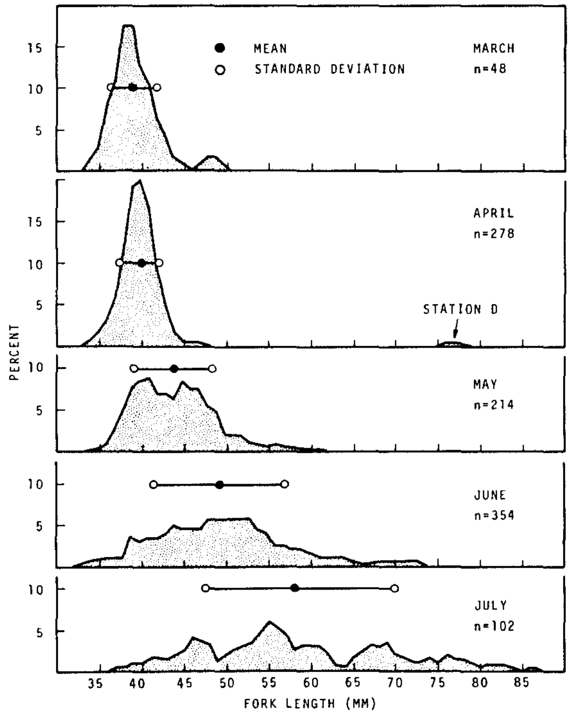


FIGURE 4.—Monthly length-frequency distributions of all juvenile chinook salmon collected at Hanford in 1969. (Data smoothed by a moving mean of three's.)

Although autochthonous insects predominated, some allochthonous terrestrial forms were ingested. The orders Homoptera, Hymenoptera, and Thysanoptera are almost entirely of terrestrial origin, and other true terrestrials occur among the adult Diptera, Coleoptera, and Lepidoptera, other than the Pyralidae (Table 1). The terrestrials were probably seized while drifting, either submerged or on the surface film. Since the river drift of allochthonous insects contributed less than 4% of the total food organisms by number, they were of relatively low value to the diet of juvenile chinook salmon in this study.

Variability in Diet

On a proportional basis, some differences in food occurred between the six primary stations and some intersite influences were evident (Table 3). Adult midges were highly utilized at Station D (70.1%), a shallow, semi-enclosed backwater area with somewhat warmer temperatures than other stations, but not larval midges (6.1%). *Notonecta* nymphs were captured primarily at Stations A (7.3%) and E (7.4%), both with extensive areas of marginal vegetation. Adult *Hydropsyche* were taken primarily at Stations B (9.2%) and C (7.2%), both with rubble substrates and partially exposed to flow of the main channel. Larval caddisflies were captured primarily at Station C (9.0%). Collembola were taken most extensively at Stations A (16.5%) and D (6.0%) where extensive mud-water interfaces existed. Proportional variations between stations were probably influenced by numerous intersite features including type of substrate, exposure to current flow, changes in seasonal and regulated water levels, and possibly feeding preferences of individual fish.

Although juvenile chinook salmon at all primary stations appeared to consume the same general types of food, Table 3 indicates some differences on the basis of relative proportions. To explore these differences more fully, the percentages of major food organisms in seven categories (adult and larval Chironomidae, Hemiptera, adult and larval Hydropsychidae, Collembola, and "all other insects") consumed within and between stations were retabulated on a monthly basis. Additionally, the samples were arbitrarily separated into "upper" (A, B, C) and "lower" (D, E, F) stations because of the distance separating them. Analysis by percent similarities (Whittaker and Fairbanks, 1958) was then applied with the formula:

TABLE 3.—Proportions of main insect groups utilized by juvenile chinook salmon at six primary stations, combined 1969 data.

Food organism	Relative proportion (%) at station:						
	A	B	C	D	E	F	Total
All Diptera	67.4	78.2	75.7	79.5	77.5	84.9	76.4
Chironomidae, adults	38.1	44.3	49.8	70.1	60.0	60.6	54.5
Chironomidae, larvae	26.6	31.1	24.3	6.1	15.9	21.9	19.6
Hemiptera (Notonectidae)	7.3	4.6	2.6	4.2	7.4	1.1	5.0
All Trichoptera	6.3	9.6	16.6	6.6	6.0	3.3	6.8
Hydropsychidae, adults	5.9	9.2	7.2	6.1	4.8	2.5	5.7
Hydropsychidae, larvae	0.0	0.1	9.0	0.2	0.2	0.0	0.6
Collembola (Hypogastruridae)	16.5	2.2	0.0	6.0	2.7	1.2	6.5
All adults[1]	73.0	67.3	64.4	91.5	82.7	76.1	78.4
All larvae[2]	27.0	32.7	35.6	8.5	17.3	23.9	21.6

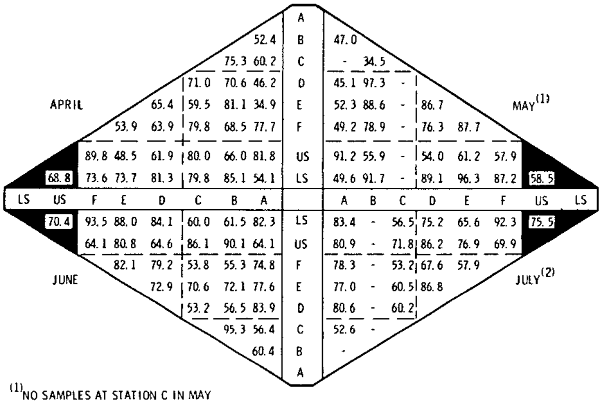
[1] Includes all winged forms, aquatic insects as well as terrestrials, plus Hemiptera and Collembola.

[2] Includes larvae, pupae, nymphs, and other stages normally associated with benthic substrates.

$$PS_c = 100 - 0.5\ \Sigma\ [a-b] = \Sigma\ \min\ (a, b);$$

where PS_c = percent similarity of community samples at different stations, and a and b are, for a given species (or group), the percentages of samples A and B which that species (or group) represents. This method, as adapted for food organisms, permits comparison of diets within stations being studied. It quantitatively measures the relative similarity in terms of species numerical composition, in this case, occurrence in the stomach contents of juvenile chinook.

Percent similarities for all possible monthly combinations of samples were compiled and entered in a diamond matrix (Figure 5). Values of combined samples for all upper and lower stations ranged from a low 58.5 in May, 68.8 in April, 70.4 in June, to 75.5 in July (dark areas).



(1)NO SAMPLES AT STATION C IN MAY
(2)NO SAMPLES AT STATION B IN JULY

FIGURE 5.—Diamond matrix comparison of percent similarities (PS_c) between and within upper (A, B, C) and lower (D, E, F) stations based on major food organisms consumed, April-July 1969.

Monthly computed figures within and between individual stations ranged above and below these values. No consistent pattern was evident. An upper station (A, B, or C) sometimes showed a high similarity value when compared with a lower station (D, E, or F) and sometimes a low value. For example, values for Station A versus F were high in April (77.7), June (74.8), and July (78.3) but low in May (49.2). The calculations were consistent with the conclusion that, despite the general similarity in diet (PS_c above 50% in most cases), proportional variations between stations occurred randomly in response to site habitat features and the feeding activity of individual fish.

Variability in Feeding Intensity

Mean numbers of insects in the stomach contents revealed an increasing trend from March to July (Figure 6). This increase corresponded with the span when fish size and water temperature were simultaneously increasing. During March and April, when fish were small and temperatures were low (3°-9°C), mean numbers of insects contained were minimum, about 10 per fish. Mean numbers increased to 38 in May and decreased to 28 in June. A peak of 47 was reached in July when the fish were large and temperatures ranged from 16° to 20°C. The May samples were influenced by high utilization of Hypogastruridae at Station A on 20 May, and the July samples by adult midges at Station F on 29 July, the last time fish were available. If these samples were excluded, mean numbers of insects contained in May and July did not

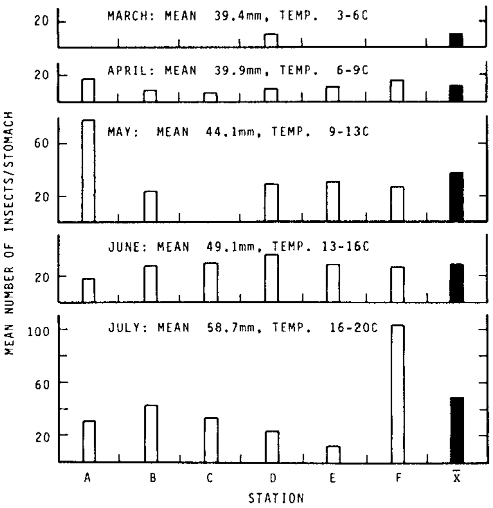


FIGURE 6.—Number of insects in stomach contents of juvenile chinook salmon at six primary stations, in relation to mean fish lengths and water temperature.

differ greatly from those in June. Yet a slight increase throughout the season was evident.

High variations within and between samples, related to feeding of individual fish, preclude meaningful comparison between stations on the basis of number of insects per stomach. Number of insects contained under field situations is, at best, a rough index to nutrition and subsequent growth. There are several reasons. First, insects vary widely in size from minute midges to large caddisflies; large number of small insects in a stomach is not necessarily equivalent to a few large insects in terms of energy supplied. Second, the relative nutritional value may vary between like amounts of different kinds of food organisms. Third, stomach contents reveal only feeding at the approximate time a sample was taken and not the preceding meals responsible for growth. Fourth, digestion rates, metabolism, and energy consumption that result in growth are highly temperature dependent, particularly over the March to July range of 2° to 20°C that occurs in the central Columbia River. Fifth, changes in water levels influence current patterns, availability of food supply and, more or less, expenditure of energy required for a fish to obtain a "full meal."

Total stomach biomass provides better information on daily rations from natural river ecosystems. Feeding intensity on the basis of the relationship between fish size and stomach biomass was calculated as:

$$FI = \frac{w}{W} \times 100;$$

where FI = feeding intensity, w = dry weight of stomach contents in grams, and W = weight of juvenile chinook salmon in grams (Olmsted and Kilambi, 1971).

Amounts of food in the stomachs of individual fish varied widely. To minimize random sample variations, feeding intensities were tabulated on the basis of combined samples for each collection date at all primary stations (Table 4). The few fish taken in March were available only at Station D, where water temperatures were somewhat higher than in the main channel due to intragravel seepage of warm water from the shoreline. These fish revealed a relatively high feeding intensity compared to fish at all primary stations in April.

FI values from grouped samples generally increased as the season progressed and the river water warmed. The highest feeding intensity in June and early July reflects primarily an increase in the size of food organisms consumed, particularly by inclusion of adult Trichoptera (Table 2).

TABLE 4.—Feeding intensity (*FI*) of juvenile chinook salmon in the central Columbia River, 1969. (Samples combined by collection date.)

Date	Number of fish	Mean fish Length (mm)	Mean fish Weight (g)	Feeding intensity (*FI*)
March 4	19	38.7	0.59	0.32
11	10	38.9	0.60	0.83
April 8	75	39.7	0.62	0.32
15	58	39.8	0.62	0.19
24	57	40.0	0.66	0.14
29	56	40.7	0.70	0.14
May 13	50	41.6	0.82	0.37
20	50	45.1	1.15	0.48
27	50	46.4	1.24	0.17
June 3	50	47.2	1.38	0.70
10	38	48.7	1.69	0.57
16	57	53.6	2.30	0.66
24	40	54.1	2.15	0.45
July 2	30	54.6	2.27	0.60
7	10	49.8	1.64	0.50
15	20	59.7	2.97	0.68
21	10	68.1	4.25	0.38
29	10	78.1	6.36	0.40

Variability in Fish Lengths

The expanding standard deviation in Figure 4 indicates an increasing size range from month to month. Lengths of juvenile chinook were relatively uniform at each station during April and early May when recruitment to shoreline zones was initiated and temperatures were low. Variations in mean fish lengths within and between stations appeared with further growth in late May, as temperatures increased, and these variations became extreme in June and July. Statistical comparison of sample mean lengths throughout the season, by Duncan's Multiple Range Test, revealed significant differences that supported this observation.

Considerable turnover of fish presumably took place along the shore during the period of high river discharge and thereafter. The inference is that groups of fish at each station were composed largely of transitory groups. Interstation turnover probably resulted from irregular movements of fish along the shoreline and seaward migration, in response to such factors as physiological stimuli, high river discharge, rising water temperature, and daily and weekly fluctuations in regulated water levels.

The combined mean lengths of fish collected at upper and lower stations provide a clearer picture of growth in relation to season (Figure 7). The slight curvilinear relationship reveals an increase in growth rates under warming temperature regimes in June and July.

Length-Weight Relationship

Although lengths of juvenile chinook salmon varied randomly between and within samples, the length-weight relationship for fish of equal size is a relatively consistent parameter. Furthermore, the relationship is characteristic of a given habitat and may indicate the adequacy of all synecological conditions leading to fish growth and development in that environment.

Preliminary statistical comparison of length-weight relationships by a nonlinear least-squares-fitted power function revealed no significant differences between stations. Consequently, the length-weight relationship of juvenile chinook salmon at Hanford was calculated by the standard regression equation $\text{Log } Y = \text{Log } A + b \text{ Log } X$. The regression was slightly curvilinear throughout the 40 to 80 mm size range (Figure 8). The computed values transform the equation to $\text{Log } \hat{Y} = -12.52 + 3.31 \text{ Log } X$.

Coefficients of Condition

In fisheries biology, the coefficient of condition is used primarily as an aid in determining the general physical status of fish stocks in different environments. The standard equation is:

$$K = \frac{W(10^5)}{L^3};$$

where K is the coefficient of condition, W is the weight of the fish in grams, L is the length of the fish in mm, and the factor 10^5 brings the value of K near unity.

Calculations were made on the basis of juvenile chinook salmon in 10-mm size groups from all primary stations combined (Table 5). K was lowest (1.08) for the 36-45 mm size group, i.e., the smallest fish emerging from the gravel in early spring and beginning to feed at low river temperatures. K values increased to the range of 1.3 to 1.4 for the larger size groups. Indices of *FI* for the

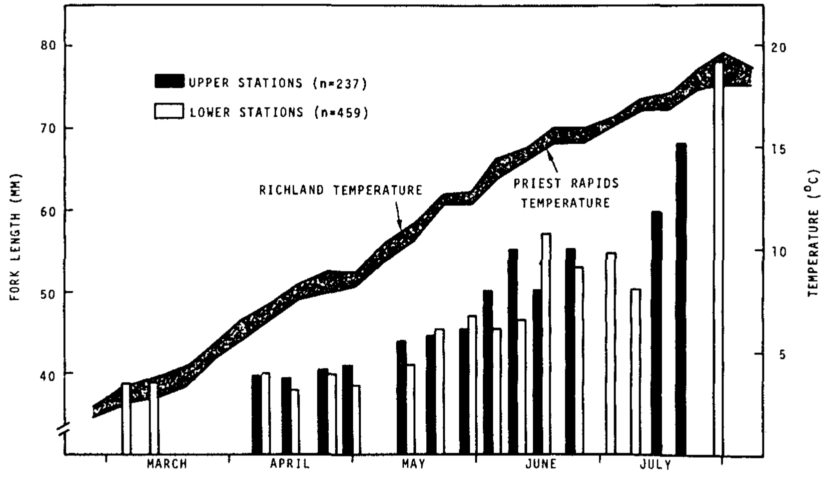


FIGURE 7.—Growth of juvenile chinook salmon at upper and lower stations, March-July 1969, in relation to Columbia River temperatures.

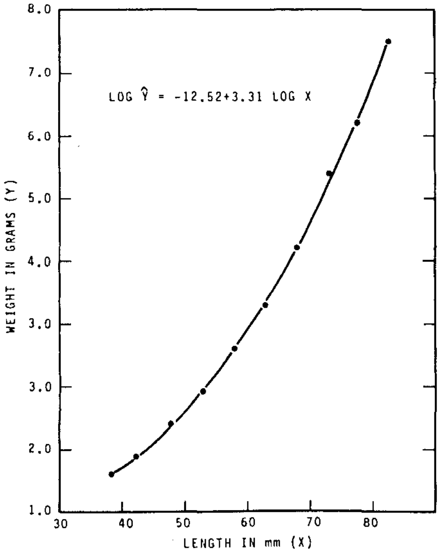


FIGURE 8.—Length-weight relationship of juvenile chinook salmon in the central Columbia River, March-July 1969.

various size groups, included in Table 5, show that the ratio of stomach food biomass to fish weight generally increases as the fish become larger. The *FI* value was low for the eight fish in the largest size group (76-85 mm) collected in late July.

DISCUSSION

Food Organisms

Distinctive features of feeding activity for juvenile chinook salmon in the central Columbia River appear to be fourfold: first, the fish utilize relatively few insect groups, predominantly Chironomidae; second, they depend largely upon autochthonous river organisms; third, they select prey drifting, floating, or swimming in the water; and fourth, they are apparently habitat opportunists to a large extent. These features are not necessarily unique among young salmonids in lotic environments. Here, in the free-flowing Columbia River, they demonstrate a close relationship with existing stream conditions.

Chironomids are of variable importance to the diet of juvenile chinook salmon in other streams. An early study conducted in the Sacramento River indicated that young chinook salmon consumed midges only to a limited extent, although floating and drifting insects did form the greatest portion of their diet (Rutter, 1904). Young chinook salmon in tributaries of the central Columbia River above Hanford in 1938 utilized few, if any, midges, although the fish fed almost exclusively on insects and the order Diptera was of greatest numerical importance (Chapman and Quistorff, 1938); these fish were relatively large, up to 152 mm, and were probably young spring chinook salmon. The food of juvenile chinook salmon in the middle Willamette River in 1958 was 39% Diptera, primarily midges, and 40% Ephemeroptera (Breuser, 1954). Emigrating chinook salmon in the lower Sacramento-San Joaquin system consumed primarily insects (90%) in 1964 but only 16% were midges (Sasaki, 1966). Adult and immature midges were a major dietary item of juvenile chinook salmon in the lower Chehalis River, along with other Diptera, Trichoptera, Plecoptera, and Ephemeroptera, in 1965 (Herrmann, 1970).

Published records reveal that insects dominate the food of other species of juvenile

TABLE 5.—Mean length, mean weight, coefficient of condition (*K*) and feeding intensity (*FI*) for 10-mm size groups of juvenile chinook salmon in the central Columbia River, March-June 1969.

Size group[1] (mm)	Number of fish	Length (mm)	Weight (g)	*K*	*FI*
36-45	411	40.5	0.72	1.08	0.33
46-55	177	50.1	1.63	1.30	0.51
56-65	57	59.1	2.76	1.34	0.55
66-75	27	70.1	4.68	1.40	0.63
76-85	8	79.0	6.53	1.33	0.25

[1] The few fish under 36 and over 85 mm in fork length were omitted.

salmonids in river habitats. However, the precise species of prey will differ between and even within various lotic systems because the existence and production of insect taxa is influenced by diverse edaphic factors.

Visual stimulation is important to the feeding of young salmonids (Chapman, 1966). Juvenile chinook salmon at Hanford exhibit considerable selection of living food organisms since nonliving material, such as insect exuviae and plant seeds, rarely occurred in their stomachs. Apparently this selection was due, in large part, to prey movement that evoked the feeding response. A preference for suspended organisms was also indicated, since benthic stages of aquatic insects were relatively unutilized by Hanford fish.

Determination of preference for a particular food organism depends on the ratios of ingredients making up the food complex and their occurrence in the stomach of fish (Allen, 1942; Ivlev, 1961). Although I obtained some invertebrate drift samples in the central Columbia River, which demonstrated an abundance of chironomid larvae, the data were inadequate for accurate determination of ratios over the entire season. Feeding apparently corresponded roughly to food organisms occurring free in the water, but not necessarily in proportion to the food actually available.

Chinook salmon fry consumed small midges most extensively whereas fingerlings tended to include larger insects in their diet. The relationship of increasing fish size to increasing food size in young salmonids has been recognized (Lindström, 1955; Hartman, 1958). Food utilized by small salmonids are subject to limitations imposed by the size of the fish whereas food utilized by larger fish can be very diverse (Mundie, 1969). However, diversity is clearly limited to what is available in a given ecosystem.

Ecological Aspects

The central Columbia River remains a large flowing river with a relatively vast water mass, rapid current velocities, and minimum shoreline habitat in relation to discharge volume. Living in stream environments requires considerable expenditure of energy that must be balanced by food consumption. Growth occurs only when energy provided by food exceeds energy expended in feeding and other activities. Energy can be conserved by juvenile salmonids in three ways: (1) leaving stream conditions to enter a lake or sea; (2) living in the stream below the main impact of the current; or (3) living predominantly in slack water, in pools, and in marginal back eddys (Mundie, 1969).

Examples of habitat selection associated with energy conservation can be noted. Young chinook salmon and steelhead trout, *Salmo gairdneri*, in Idaho streams inhabit velocities and depths in relation to body size, shifting to faster and deeper water as growth occurs (Chapman and Bjornn, 1969; Everest and Chapman, 1972). Similarly, chinook salmon fry in the Big Qualicum River, British Columbia, occupy marginal areas while the larger fish move into habitats of progressively higher velocity (Lister and Genoe, 1970). Since my samples were obtained entirely from shoreline areas that could be effectively seined, they reflect feeding in those habitats. A possible shift of larger fish to deep water would remain undetected.

Because metabolic rates of cold-blooded animals such as fish increase as temperatures rise, more food must be consumed for growth of juvenile chinook salmon to be maintained as the season advances and the water warms. My data show that feeding intensity, on the basis of both number of insects and total stomach biomass, tended to increase from March to July.

Although chironomids are small and individually low in nutritional value, they are utilized throughout the season by juvenile chinook at Hanford and their abundance compensates for a lack of size. The adult caddisflies appearing in June and July are large and provide greater nutritional value per individual at a time when temperatures are high and more energy is required for fish growth. By dry weight, 1 adult *Hydropsyche cockerelli* is equal to 35 adult midges. Although the calories available per gram of dry weight for chironomids (5,424) and hydropsychids (5,386) are nearly equal (Cummins and Wuycheck, 1971), considerably less energy is required to capture 1 prey organism than 35.

Invertebrate drift is important to the feeding of stream fish, and particularly so at Hanford. The significance of the drift phenomenon is that of increasing the availability of food and supplementing possible site limitations on insect production; moreover, under conditions of high discharge, the quantity of drift organisms passing downriver per unit of time is higher than under low flow conditions (Waters, 1969). If this is true for the central Columbia River, the annual spring spate increases the availability of food organisms to juvenile chinook salmon during their period of maximum abundance.

Changes in river water levels, both seasonal and regulated, appear to have unique significance at Hanford by exerting an influence on populations of aquatic insects and juvenile chinook salmon in inshore areas. The influence is apparent in at least four theoretical ways.

First, the annual increase in river discharge in April and May (Figure 2) inundates barren shoreline areas that are exposed to air during the preceding winter. Recolonization of flooded inshore areas by aquatic insects depends upon larvae in the drift, which may occur rapidly, or upon the deposition of eggs by adults. There are no available data on recolonization rates of recently inundated areas at Hanford. But detached insect larvae usually spend only a short time in the drift and re-attach as soon as possible (Elliott, 1967).

Second, weekly and daily variations in water level resulting from flow regulation at Priest Rapids Dam (Figure 3), which periodically floods and exposes vast stretches of shoreline areas, restricts insect recolonization and incorporates marginal dwellers into the river drift. On this basis, it is not surprising that the diet of juvenile chinook salmon includes food organisms that normally live along the shoreline such as *Notonecta* nymphs, adult springtails, and terrestrial Arachnida (spiders).

Third, station occupation by juvenile chinook salmon appears to be temporally limited. Young salmonids commonly occupy relatively small home areas (ecological niches) for a period of feeding and growth prior to seaward migration (Chapman, 1966; Edmondson, Everest, and Chapman, 1968; Chapman and Bjornn, 1969). Analysis of data from fish collected at the primary stations reveals considerable variation in sizes from week to week after mid-May. At least part of this variation must result from weekly changes in regulated water level at Priest Rapids Dam (up to 2 m in 24 hr on weekends) that implements population turnover.

Fourth, the eminent decline in river discharge volume from the annual spring spate (> 300,000 cfs) to the summer period of low flow(≃40,000 cfs) suggests that the falling water level is one factor involved in prompting seaward juvenile chinook salmon still lingering at Hanford. At any rate, the seasonal increase and then decrease in river flows accompanied by rising temperatures (Figure 2) are the main environmental factors correlated with seaward migration. These phenomena, which have occurred annually throughout recorded history, may well have played an evolutionary role in the development of the spring migration characteristic for young fall chinook salmon produced in the Columbia River ecosystem.

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