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FOOD HABITS OF MIGRATING SALMONID SMOLTS PASSING BONNEVILLE DAM IN THE COLUMBIA RIVER, 1984

WILLIAM D. MUIR and ROBERT L. EMMETT

Coastal Zone and Estuarine Studies Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, Washington 98112, U.S.A.

ABSTRACT

The food habits of migrating juvenile steelhead (*Salmo gairdneri*), sockeye salmon *(Oncorhynchus nerka)*, coho salmon *(O. kisutch)*, and chinook salmon *(O. tshawytscha)* were identified from April through August 1984 at Bonneville Dam in the Columbia River. During the spring (April–June), the gammarid amphipods *Corophium salmonis* and *C. spinicorne* were the dominant prey for all species. Many insect taxa were also consumed, but in small quantities. Significant diet overlap occurred between all species during the spring due to the importance of *Corophium*. In summer (July–August), the importance of *Corophium* declined in the diet of subyearling chinook salmon and was replaced with *Daphnia* spp. and adult dipterans (primarily chironomids).

KEY WORDS Salmonid smolts Food habits Diet overlap *Corophium* Reservoir Diet diversity

INTRODUCTION

Pacific salmon *(Oncorhynchus spp.)* and steelhead *(Salmo gairdneri)* in the Columbia River system make important contributions to offshore and riverine fisheries, both sport and commercial (Chaney and Perry, 1976; Bohn and McIssac, 1983). However, mainstem dams and impoundments reduce the number of salmon and steelhead because of increased mortality of seaward migrating smolts, due in part to increased travel time through reservoirs (Ebel, 1977; Raymond, 1979). For salmonids emigrating from the upper Snake and Columbia Rivers, this could mean migrating through an excess of 500 km of slack water.

Substantial losses of energy reserves occur during seaward migrations; prolonged migrations further increase the energy demands of smolts (Rondorf *et al.,* 1985). Because migrating salmonid smolts actively feed during seaward migration to help offset this depletion of energy reserves, the quantity and quality of prey consumed could ultimately influence survival. Food habits of juvenile salmonids have been studied in free-flowing riverine (Chapman and Quistorff, 1938; Becker, 1973; Craddock *et al*., 1976) and estuarine environments (McCabe *et al*., 1983, 1986) of the Columbia River and other systems (Breuser, 1961; Sasaki, 1966; Herrmann, 1971; Loftus and Lenon, 1977; Reimers *et al*., 1978; Meyer *et al*., 1981). However, we are unaware of any published food habit information for migrating salmonid smolts in reservoirs. This paper helps fill that void. Specific objectives were to determine the following: (1) what prey items were eaten, (2) seasonal changes in diet, and (3) diet overlap between species of juvenile salmonids.

METHODS

Sampling was done at Bonneville Dam, the lowermost dam on the Columbia River (Figure 1). The outmigration of salmonid smolts usually begins in late April, peaks in May, and then declines for all species except subyearling chinook salmon *(O. tshawytscha)* which continue to migrate into the fall (Park,

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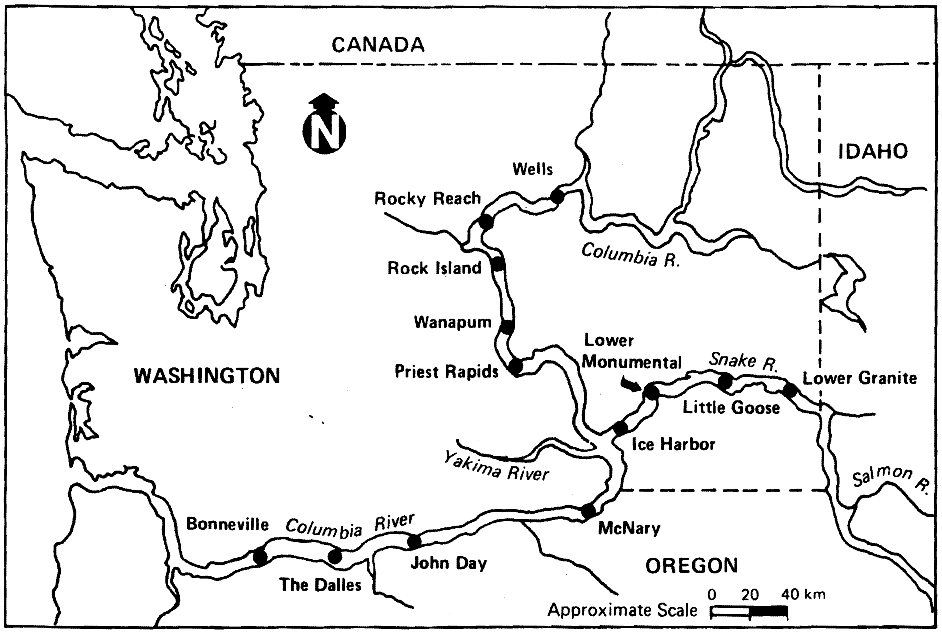

Figure 1. The Columbia and Snake River system showing Bonneville Dam and other points of interest

1969; McConnaha *et al.*, 1985). The smolt outmigration generally occurs during the period of increasing river flow and rising water temperature (Mains and Smith, 1964).

River flows vary annually, but generally are highest during the spring freshet (April–June) and decline rapidly in July. During the 1984 study period (25 April to 15 August), flows ranged from 10·5 m^3/second (1000) during the week of 20 June (7-day average) to 4·1 m^3/second (1000) during the week of 8 August (Figure 2). Reservoir water temperatures steadily increased from 10·2 C the week of 25 April to 21·2 C by the week of 15 August (Figure 2).

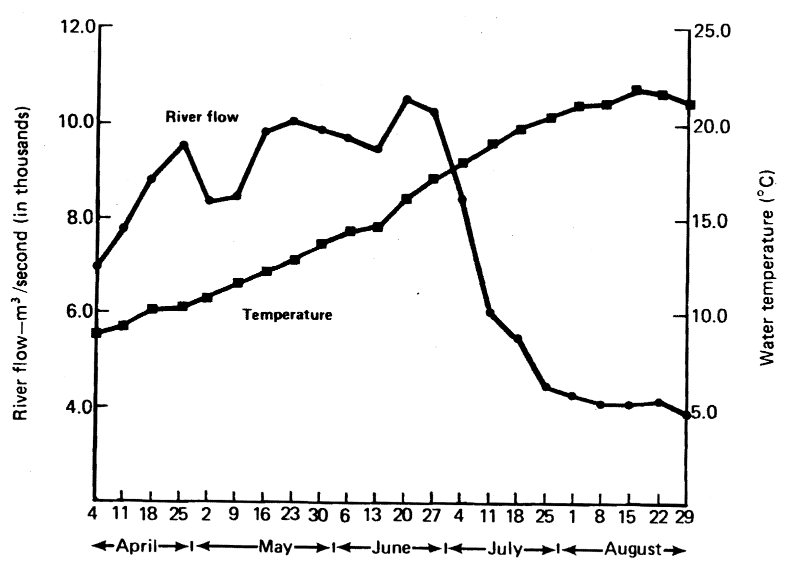

Figure 2. Water temperatures and river flows at Bonneville Dam during spring and summer, 1984

Sampling

Salmonids for this study were collected at Bonneville Dam's Second Powerhouse during an evaluation of the juvenile downstream bypass system (Gessel *et al*., 1985). The majority of the specimens were freshly killed fish from vertical distribution tests conducted in turbine intakes. During weeks when vertical distribution tests were not conducted, or sufficient numbers of a particular species were unavailable, additional specimens of freshly killed fish were collected in a juvenile bypass trap (Gessel *et al*., 1985). Chinook salmon were separated into yearling and subyearling age groups using length frequency distributions. We attempted to collect 20 fish of each species weekly. These salmonids were downstream migrants originating upstream from Bonneville Dam. No attempt was made to distinguish between hatchery or wild fish.

Fish were injected with an 8 per cent buffered formaldehyde solution (Emmett *et al*., 1982) as soon after capture as possible. After 24 hours, fish were measured (fork length) and their stomachs removed and stored in 70 per cent ethyl alcohol. Stomach contents were identified to the lowest practical taxon with the aid of a 10X microscope. Insects were further subdivided by life stage, i.e. adult, pupa, and larva. Prey items were weighed to the nearest 0·0001 g after blotting and air drying for 10 minutes. When prey items were broken (frequently with dipterans), head capsules were counted, and body parts were combined for weighing.

Data Analysis

The Index of Relative Importance (*IRI*) developed by Pinkas *et al.* (1971) was used to assess the diet of salmonids:

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

where N = numerical percentage of a prey item,
W = weight percentage of a prey item,
F = frequency of occurrence of a prey item.

IRI values were then converted to percentages.

To compare diet diversity, the Shannon-Weaver Diversity Index (H') was used (Shannon and Weaver, 1963). The formula is $H' = -\Sigma P_i(\log_2 P_i)$, where P_i = the per cent *IRI* of a food item. The H' index provides a diversity value ranging from 0·0 (low diversity) to >6·0 (high diversity) and is influenced by both the number of taxa and the evenness with which they occur.

To measure diet overlap between species, the equation developed by Morisita (1959) and modified by Horn (1966) utilizing *IRI* values (Wallace 1981) was used:

$$C = \frac{2\sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

where C = overlap coefficient,
s = food categories,
X_i = per cent *IRI* of fish species X contributed by food category i,
Y_i = per cent *IRI* of fish species Y contributed by food category i.

Values of C can range from 0 (no overlap) to 1 (complete overlap), with a value of 0·6 considered significant (Zaret and Rand, 1971).

IRI, H', and C values were calculated for each species on a weekly basis and for all weeks combined. Subyearling chinook salmon captured after the spring outmigration were analysed separately to avoid distorting their diet in the spring for comparison to other salmonid species.

RESULTS

During the spring outmigration (April–June), 592 stomachs were examined including 109 steelhead, 135 sockeye salmon (*O. nerka*), 94 coho salmon (*O. kisutch*), 130 yearling chinook salmon, and 124 subyearling chinook salmon. An additional 94 subyearling chinook salmon stomachs were examined in July and August. Approximately 95 per cent of all the stomachs contained identifiable food items representing a variety of taxa.

Steelhead

Although steelhead ate a wide variety of prey (Table I), the gammarid amphipods *Corophium* spp. were the major portion (99 per cent *IRI*) of their diet (Figure 3). *C. salmonis* was eaten almost exclusively in early May, with *C. spinicorne* becoming increasingly important in late May and June (Figure 4). Fish were unimportant in the diet, with only one small subyearling chinook salmon being found. Insects were eaten frequently, but in small quantities.

Sockeye salmon

Sockeye salmon (Figure 3) preyed heavily on *Corophium* spp. (83 per cent *IRI*) as well, and also ate dipteran adults (6 per cent *IRI*) and homopterans (8 per cent *IRI*). The dipterans were primarily emerging chironomids; however, larvae and pupae were also eaten (Table I). The homopterans were represented by Cicadellidae (leaf hoppers), Psyllidae (psyllids), and Aphididae (aphids). Both homopterans and dipterans were important in May, but declined in importance in June (Figure 4). Zooplankters were also utilized by sockeye salmon, but infrequently.

Coho salmon

Overall, *Corophium* spp. represented 94 per cent (*IRI*) of the diet for coho salmon (Figure 3), with *C. salmonis* being utilized in early May and a combination of *C. salmonis* and *C. spinicorne* in late May and June (Figure 4). Hymenopterans, primarily terrestrial ants (Formicidae), were important during some weeks (Figure 4); however, they only contributed 4 per cent of the total *IRI*. Various other insects were eaten, but in small quantities (Table I).

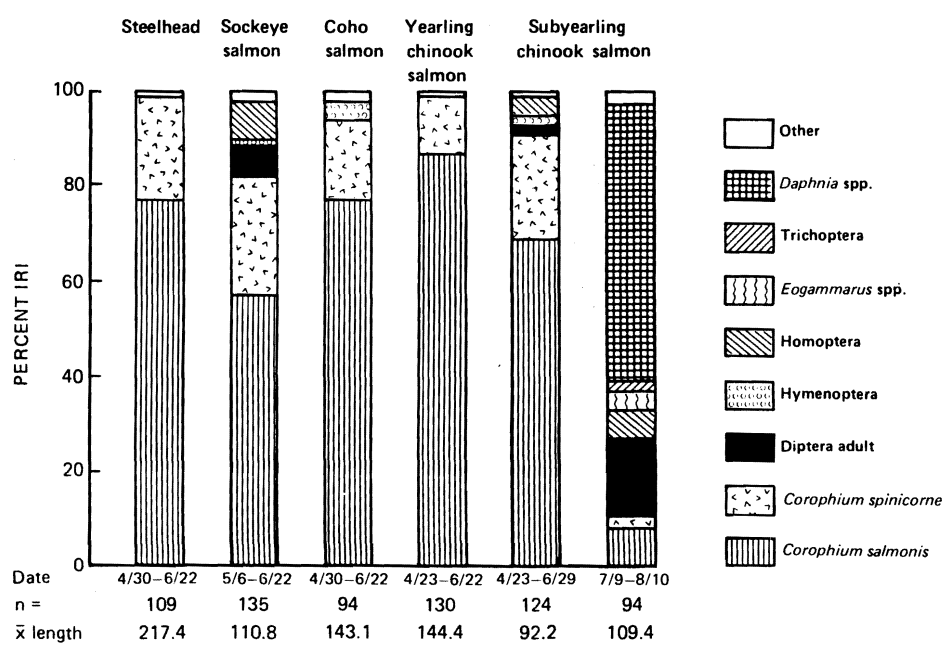

Figure 3. Diets (% *IRI*) of migrating juvenile salmonids collected at Bonneville Dam during 1984. Only prey items having an overall *IRI* value ≥1 per cent are shown. Mean lengths in mm

Table I. The per cent frequency of occurrence of food items in juvenile salmonid stomachs collected at Bonneville Dam during 1984. Sample size is shown in ( )

Food item	Yearling chinook (130)	Coho (94)	Sockeye (135)	Steelhead (109)	Subyearling chinook (124)	Subyearling chinook (94)*
Gastropoda				1·1		
Bivalvia						
Corbicula manilensis		1·1	0·8	3·3	0·8	1·1
Crustacea						
Mysidacea						
Neomysis mercedis						3·4
Amphipoda						
Eogammarus spp.	14·3	20·9	18·1	15·8	23·8	25·8
Corophium salmonis	90·8	82·4	94·0	91·6	92·6	56·2
Corophium spinicorne	60·5	63·7	84·2	73·7	63·1	29·2
Decapoda						
Pacifasticus spp.	2·5	1·1	1·5	2·1		1·1
Cladocera						
Daphnia spp.			0·8			52·8
Bosmina spp.			1·5			1·1
Copepoda						
Calanoida			3·0			3·4
Cyclopoida			6·0			18·0
Insecta						
Diptera adults	14·3	29·7	41·4	11·6	45·1	70·8
Diptera pupae	10·1	14·3	29·3	9·5	28·7	47·2
Diptera larvae	8·4	2·2	11·3	3·2	9·0	3·4
Trichoptera adults	0·8		1·5	4·2	2·5	39·3
Trichoptera larvae				6·3	0·8	1·1
Pscoptera adults	0·8	3·3	6·0	2·1	5·7	23·6
Lepidoptera adults						1·1
Lepidoptera larvae			0·8			
Thysanoptera adults			3·0			2·3
Coleoptera adults	5·9	8·8	9·0	6·3	12·3	14·6
Coleoptera larvae		1·1				
Hymenoptera adults	14·3	31·9	28·6	9·5	25·4	15·7
Hemiptera	1·7	2·2	2·3	1·1	5·7	19·1
Homoptera adults	12·6	24·2	38·4	7·4	30·3	59·6
Ephemeroptera	6·7	2·2	14·3	4·2	13·1	12·4
Unidentified insects	4·2	3·3	4·5	3·2	2·5	2·3
Arachnida	4·2	6·6	12·0	3·2	11·5	9·0
Osteichthys						
Salmonidae				1·1		
Digested fish	0·8		0·8			2·2
Plant material	5·9	12·1	4·5	11·6	2·5	7·9

*Subyearling chinook salmon collected in July and August were analysed separately.

Yearling chinook salmon

Corophium spp. were also the most important prey (97 per cent *IRI*) for yearling chinook salmon (Figure 3). During most of May, *C. salmonis* represented a large portion of the diet, but in late May and June, *C. spinicorne* increased in importance (Figure 4). Hymenopterans were also important in June.

Subyearling chinook salmon

During the spring outmigration, subyearling chinook salmon (Figure 3) fed intensively on *Corophium* spp. (90 per cent *IRI*); however, they also utilized dipteran adults (2 per cent *IRI*), hymenopterans (3 per

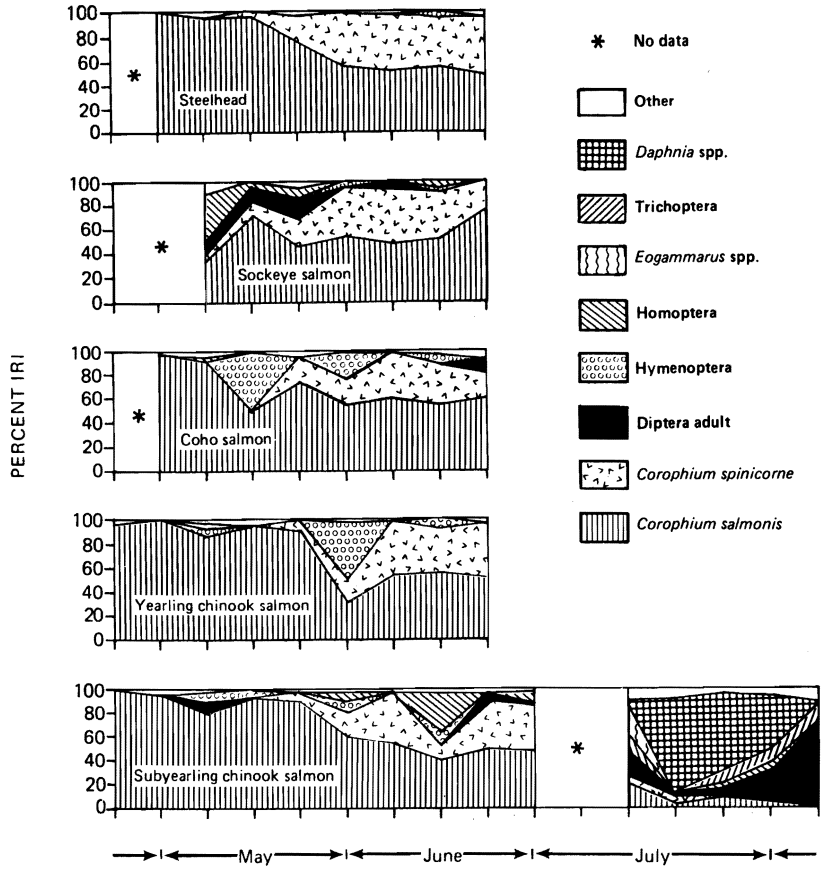

Figure 4. The seasonal food habits (% *IRI*) of migrating juvenile salmonids collected at Bonneville Dam during 1984. Only prey items having an *IRI* value ≥3 per cent are shown

cent *IRI*), and homopterans (4 per cent *IRI*). During May, *C. salmonis* was the chief prey item; in June, *C. spinicorne*, homopterans, and hymenopterans were also consumed (Figure 4). Dipterans (Chironomidae) were eaten frequently during spring, but in small quantities (Table I).

During the summer (July and August), the importance of *Corophium* spp. in the diet declined dramatically (11 per cent *IRI*) and was replaced with *Daphnia* spp. (58 per cent *IRI*), dipteran adults (16 per cent *IRI*), and other invertebrates (Figure 3). During the three weeks in July that *Daphnia* spp. were important, water temperatures were 20–21°C. Dipteran adults (Chironomidae) were the most important food in August (Figure 4).

Diet diversity

All species had low to moderate diet diversity largely due to the predominance of *Corophium* spp. (Figure 5). Sockeye salmon had the highest average H' (2·77), followed by subyearling chinook salmon (2·25) and coho salmon (1·68). Diet diversity was lowest for steelhead and yearling chinook salmon, 1·47 and 1·23, respectively. In general, the smaller species (sockeye and subyearling chinook salmon) ate greater numbers of smaller prey such as dipterans, homopterans, and zooplankters along with *Corophium* spp., whereas the larger salmonids (steelhead and yearling chinook salmon) concentrated on the relatively larger *Corophium* spp. (Table I).

Seasonally, diet diversity increased during May and June for all species except sockeye salmon, whose H' peaked in early May and declined to its lowest point in late June (Figure 5). Except for sockeye salmon, weekly changes in H' were similar for all species, indicating prey availability influenced feeding. For example, all of the salmonids began consuming *C. spinicorne* at about the same time (Figure 4).

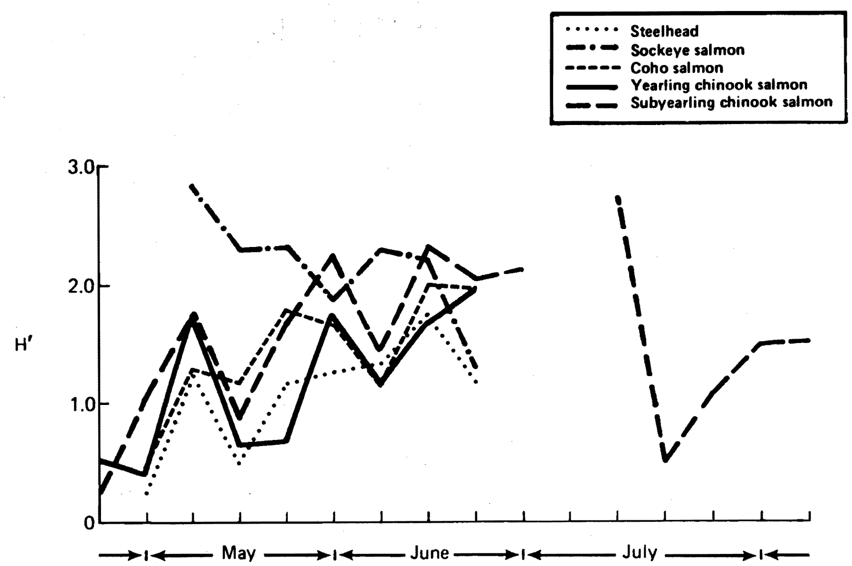

Figure 5. The Shannon–Weaver Diversity Index (H') for the diets of migrating juvenile salmonids collected at Bonneville Dam during 1984

Diet overlap

Diet overlap was high, averaging ⩾ 0·90 for all the species during the spring outmigration (Table II). All the values were significant (⩾0·60), except for the overlap between steelhead and sockeye salmon during one week in early May (0·57). These high C values resulted from low diet diversity caused by dependence on *Corophium* spp. Sockeye salmon had the highest diet diversity (H') and correspondingly had slightly lower diet overlaps with other species.

Table II. Diet overlaps (C) between migrating juvenile salmonids collected at Bonneville Dam during 1984. Single values represent overall overlap value and double values represent the seasonal range. $C \geq 0{\cdot}60$ is considered a significant diet overlap (Zaret and Rand, 1971)

Species	Subyearling chinook	Yearling chinook	Coho	Sockeye	Steelhead
Subyearling chinook	1·00	0·97	0·99	0·98	0·99
Yearling chinook	0·67–1·00	1·00	0·99	0·90	0·98
Coho	0·71–1·00	0·68–1·00	1·00	0·94	1·00
Sockeye	0·63–0·99	0·61–0·99	0·60–0·99	1·00	0·95
Steelhead	0·74–1·00	0·61–1·00	0·68–1·00	0·57–1·00	1·00

DISCUSSION

In free-flowing sections of the Columbia River and other river systems, juvenile salmonids feed predominantly on insects. In tributaries of the upper Columbia River, Chapman and Quistorff (1938) found a wide variety of insects in the stomachs of juvenile chinook and sockeye salmon and steelhead. Becker (1973) reported that dipteran adults (mostly chironomids) were the most important food for subyearling chinook salmon in the Hanford area of the upper Columbia River (Figure 1). In the Prescott–Kalama area (below Bonneville Dam), Craddock *et al.* (1976) found subyearling chinook salmon utilizing *Daphnia* spp. from July through October and insects in spring and fall. Chironomids and ephemeropterans were most important for juvenile coho and chinook salmon in small tributaries in Oregon (Breuser, 1961) and for juvenile chinook salmon in the Salcha River, Alaska, (Loftus and Lenon, 1977). Amphipods were unimportant in all of the above studies.

In the Columbia River estuary (McCabe *et al.*, 1983); the Sacramento–San Joaquin Delta, California (Sasaki, 1966); the Sixes River, Oregon (Reimers *et al.*, 1978); Grays Harbor, Washington (Herrmann, 1971); Duwamish estuary, Washington (Meyer *et al.*, 1981); and other Pacific Northwest and Canadian estuaries not cited, *Corophium* spp. were the major food for juvenile salmonids. Insects were of secondary importance (especially chironomids), increasing in importance in the upper estuarine areas. In the Columbia River estuary, *Daphnia* spp. were important prey for subyearling chinook salmon in summer (McCabe *et al.*, 1983). The food habits of salmonid species in the Columbia River estuary as reported by McCabe *et al.* (1983) are nearly identical to those described here, both in the types of foods eaten and their seasonal occurrence, while being considerably different from those reported from free-flowing riverine areas.

Becker (1973) reported that subyearling chinook salmon in the Hanford reach of the Columbia River showed a preference for suspended, moving organisms, since benthic stages of aquatic insects and nonliving material such as plant seeds and insect exuviae rarely occurred in stomachs. Why then is *Corophium*, a tube-dwelling benthic invertebrate, so extensively utilized by salmonids passing through Bonneville reservoir? *Corophium salmonis* reportedly undergo vertical migrations, both daily and seasonally, with migrational peaks occurring in the evening hours and during spring months (Davis, 1978; Wilson, 1983). These migrations, coupled with higher river flows during the spring, may keep these amphipods suspended in the water column for long periods of time, thus making them susceptible to predation by salmonids. In the Duwamish estuary (Meyer *et al.*, 1981), the Columbia River estuary (McCabe *et al.,* 1983), and Bonneville reservoir (this study), the importance of *Corophium* declined in summer as river flows declined. Meyer *et al.* (1981) also reported that the proportion of *Corophium* in the diet of salmonids was highest in the evening and lower during the day when the proportion of insects in the diet increased. Therefore, *Corophium* availability probably peaks in spring during the major salmonid outmigration and coincides with the peak feeding times (evening) of juvenile salmonids (Johnson and Johnson, 1981; Rondorf *et al.*, 1985).

Kolok and Rondorf (1987) found that the caloric density (Kcal g^{-1} dry weight) of prey items consumed by yearling chinook salmon was lower when *Corophium* were abundant in the diet. This decrease in caloric value may be offset by the abundance of *Corophium,* resulting in decreased searching and handling times. Fish typically respond to high levels of food availability by narrowing their diets (Werner and Hall, 1974; Dill, 1983). In Bonneville reservoir, salmonids had low diet diversity (diet breadth) and correspondingly high diet overlap between species during the spring outmigration, indicating abundant prey. In summer, when subyearling chinook salmon consumed less *Corophium,* their diet breadth increased, indicating reduced *Corophium* availability.

During 1984, over 32 million juvenile salmonids were released from hatcheries into the Bonneville reservoir (McConnaha *et al.*, 1985). In addition, releases from hatcheries upstream from Bonneville reservoir and an unknown number of wild salmonids passed through the reservoir. What effect juvenile salmonid feeding had on the reservoir's food resources, especially *Corophium*, is unknown. Levings and Levy (1977) and Nelson (1979) showed that fish predation could be a governing factor in estuarine amphipod populations. The fact that *Corophium* were intensively harvested by salmonids in Bonneville reservoir for the entire spring outmigration suggests that the *Corophium* population was not overharvested during that period.

Corophium spp. are typically characterized as brackish water invertebrates which can tolerate fresh water (Green, 1968) and are not included in most standard freshwater invertebrate texts (Pennak, 1978; Ward and Whipple, 1945). In the Columbia River, *Corophium* spp. have been reported to occur as far upstream as John Day reservoir (Kolak and Rondorf, in press). In Bonneville reservoir they seem to be the dominant macroinvertebrate fauna (this study). How *Corophium* became established upstream of tidal influence is unknown. In the Soviet Union, brackish water invertebrates (including *Corophium* spp.) are routinely introduced into freshwater reservoirs to increase reservoir productivity where they often become the dominant invertebrate species (Yanushevich, 1963). *Corophium* spp., particularly *C. salmonis*, require fine sandy sediments for benthic habitat. Before the construction of Bonneville Dam, this type of substrate was probably limited; however, impounding resulted in reduced velocities and increased sedimentation, which in turn probably increased the habitat for *Corophium* spp.

This study showed that juvenile salmonids were utilizing the Bonneville reservoir as a feeding area, as evidenced by the low percentage of empty stomachs. Since size apparently affects a smolt's ability to survive in seawater (Wagner *et al.*, 1969; Mahnken *et al.*, 1982), information on how well their dietary requirements are being met during reservoir migration is needed. Since *Corophium* spp. are so important to migrating juvenile salmonids in the Bonneville reservoir, information on the life histories, distributions, and abundances of *Corophium* and other invertebrates in the reservoir would be valuable to resource and hatchery managers responsible for maintaining and enhancing Columbia River salmonid runs. To the authors' knowledge no information of this type currently exists for the area upstream from Bonneville Dam.

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