

Food Habits of Juvenile American Shad and Dynamics of Zooplankton in the Lower Columbia River

Abstract

As many as 2.4 million adult American shad annually pass John Day Dam, Columbia River to spawn upriver, yet food web interactions of juvenile shad rearing in John Day Reservoir are unexplored. We collected zooplankton and conducted mid-water trawls in McNary (June-July) and John Day reservoirs (August-November) from 1994 through 1996 during the outmigration of subyearling American shad and Chinook salmon. Juvenile American shad were abundant and represented over 98% of the trawl catch in late summer. The five major taxa collected in zooplankton tows were *Bosmina longirostris*, *Daphnia*, cyclopoid copepods, rotifers, and calanoid copepods. We evaluated total crustacean zooplankton abundance and *Daphnia* biomass in relation to water temperature, flow, depth, diel period, and cross-sectional location using multiple regression. Differences in zooplankton abundance were largely due to differences in water temperature and flow. Spatial variation in total zooplankton abundance was observed in McNary Reservoir, but not in John Day Reservoir. Juvenile American shad generally fed on numerically abundant prey, despite being less preferred than larger bodied zooplankton. A decrease in cladoceran abundance and size in August coupled with large percentages of *Daphnia* in juvenile American shad stomachs indicated heavy planktivory. Smaller juvenile American shad primarily fed on *Daphnia* in August, but switched to more evasive copepods as the mean size of fish increased and *Daphnia* abundance declined. Because *Daphnia* are particularly important prey items for subyearling Chinook salmon in mainstem reservoirs in mid to late summer, alterations in the cladoceran food base is of concern for the management of outmigrating salmonids and other Columbia River fishes.

Introduction

Hydroelectric development has impounded much of the Columbia River, which has enabled zooplankton communities to become well established in main-stem reservoirs. Zooplankton is an important food source for many resident and anadromous fishes that rear and migrate through Columbia River reservoirs (Craddock et al. 1976; Dauble et al. 1980; Beckman et al. 1985; Rondorf et al. 1990). The need for more information on Columbia River zooplankton has increased due to the proliferation of a non-native planktivore, American shad (*Alosa sapidissima*) (Petersen et al. 2003). Subyearling Chinook salmon (*Oncorhynchus tshawytscha*) is the salmonid species most dependent upon zooplankton prey as they exhibit extended rearing and feeding in main-stem shoreline habitats (Rondorf et al. 1990). The Hanford Reach of the Columbia River produces 10-30 million subyearling Chinook salmon fry annually (Paul Hoffarth, Washington Department of Fish and Wildlife, personal communication), many of which rear in McNary (Key et al. 1994)

and John Day reservoirs (Miller and Sims 1984). Hanford Reach Chinook salmon are important because they represent the majority of naturally reproducing fall run Chinook salmon in the Columbia River Basin (Huntington 1996; Dauble and Watson 1997).

Daphnia is a common cladoceran prey item for subyearling Chinook salmon rearing in McNary Reservoir (Rondorf et al. 1990). They are exploited heavily during the summer by subyearlings not only in McNary Reservoir, but also in other lower Columbia River reservoirs and the estuary (Craddock et al. 1976; Kirn et al. 1986; Muir and Emmett 1988). Subyearling Chinook salmon are opportunistic feeders and their use of *Daphnia* reflects the seasonal availability of these larger-bodied zooplankters. Despite the importance of zooplankton as prey, the study of zooplankton population dynamics in main-stem Columbia River reservoirs during subyearling rearing and seaward migration has received little attention. Competition for prey between juvenile salmonids and juvenile American shad may now be occurring in lower Columbia River reservoirs.

American shad are native to the east coast of North America where they occur in rivers from

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Florida to New Brunswick, Canada, but have become numerous after their introduction to the west coast. Introduced into the Sacramento River, California, in 1871, American shad quickly expanded their range northward along the Pacific Coast and were collected in the Columbia River as early as 1877. Concurrently, millions of American shad fry were stocked in the lower Columbia River, Willamette River, and the Snake/Columbia River confluence from 1885 to the early 1900's (Lampman 1946). Adult returns of American shad increased markedly with the installation of fish ladders at hydroelectric dams and the inundation of Celilo Falls in 1957, which apparently blocked upstream migration of American shad. By the 1960's, the first annual adult return of 100,000 American shad was recorded at Bonneville Dam. In 2005, over 6 million adult American shad returned to the Columbia River (University of Washington 2005), most of which passed John Day Dam to spawn in John Day and McNary reservoirs. In contrast, about 1.2 million salmon returned to the Columbia River in 2005, whereas historically the number was 10-16 million (Ebel et al. 1989).

The recent increase of juvenile American shad in the Columbia River has raised concern over their role as potential competitors with juvenile salmon for prey. Like Pacific salmon, American shad are anadromous, and like subyearling Chinook salmon in particular, American shad juveniles rear in mainstem reservoirs and typically outmigrate as subyearlings. Because juvenile American shad opportunistically feed on zooplankton and aquatic insects in other river systems where they are native, they are likely exploiting food resources similar to those used by subyearling Chinook salmon in the lower Columbia River. In the Delaware River, Pennsylvania, juvenile shad predominately consume chironomids (Ross et al. 1997), while in the Connecticut River, larval shad consume *Bosmina*, cyclopoid copepodites, and chironomid larvae (Crecco and Blake 1983). High densities of juvenile American shad in John Day Reservoir may have the potential to alter the zooplankton community through size selective grazing.

We investigated zooplankton population dynamics in McNary and John Day reservoirs during the period of subyearling Chinook salmon rearing and emigration. We also explored the food habits of juvenile American shad to compare zooplankton consumption with prey availability. Our study

had three primary objectives: (1) describe the composition and abundance of zooplankton taxa in McNary and John Day reservoirs; (2) describe temporal and spatial dynamics in crustacean zooplankton abundance and *Daphnia* biomass; and (3) identify the effects of juvenile American shad feeding on the zooplankton community in John Day Reservoir.

Methods

Study Area

We conducted our study in two mainstem impoundments of the Columbia River, McNary and John Day reservoirs. Study areas were located between river kilometer (rkm) 381 and 391 in John Day Reservoir and between rkm 470 and 514 in McNary Reservoir (Figure 1). McNary Reservoir is the first impoundment downstream of the Hanford Reach of the Columbia River and the confluence of the Columbia and Snake rivers. It is 98 km long, has a surface area of 122 km², a mean depth of 11 m, and a maximum depth of 35 m. John Day Reservoir, immediately downstream of McNary Reservoir, is 122 km long, has a surface area of 198 km², a mean depth of 15 m, and a maximum depth of 55 m. Water temperatures in McNary and John Day reservoirs generally range from 2 to 21°C annually and exhibit little thermal stratification. McNary and John Day reservoirs are run-of-the-river reservoirs with little storage capacity and mean retention times of 4.0 and 7.3 d, respectively (Ebel et al. 1989). Grand Coulee Dam (rkm 960), which has a mean retention time of 45 d, generally regulates the flow of downstream impoundments, affecting both McNary and John Day reservoirs.

Sample Collection

During 1994-1996, we collected zooplankton weekly during June and July in McNary Reservoir and every other week from August to November in John Day Reservoir. The beginning and ending dates of zooplankton collection were seasonally timed to coincide with the outmigration of subyearling Chinook salmon in McNary and John Day reservoirs. An important component of our sampling design was to move zooplankton sampling downstream from McNary to John Day Reservoir as subyearling Chinook salmon left McNary Reservoir and entered John Day Reservoir. We conducted trawling to assess the presence

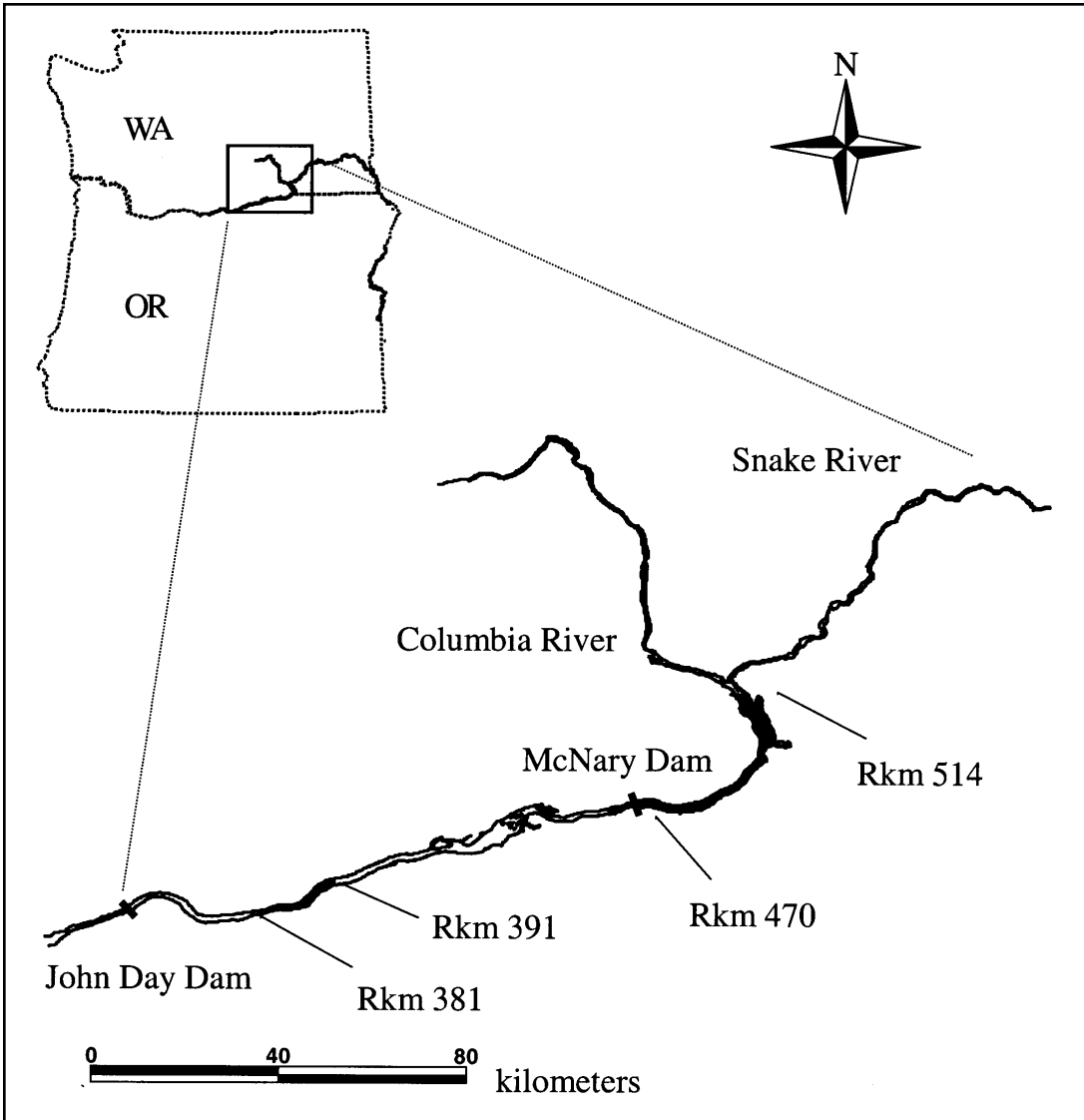


Figure 1. Sampling areas for zooplankton collection in John Day and McNary reservoirs of the Columbia River.

of juvenile salmon and juvenile American shad in our study area. The seasonal outmigration of subyearling Chinook salmon varied from year to year, as did our zooplankton collection dates.

We collected zooplankton samples using paired Miller samplers fitted with 153 μm mesh nylon nets and internally mounted flow meters to estimate the water volume sampled (Miller 1961). The samplers were towed horizontally through the water and parallel to the shoreline in an upstream direction for 5 min. Filtered samples

were preserved in 10% formalin and dyed with rose bengal stain to facilitate identification of zooplankton in the laboratory.

Zooplankton samples were collected at cross-sectional transects designated by river kilometer. Transects were randomly selected without replacement from all possible transects (every 0.16 km) within the study area during each sample period. The number of transects sampled during each sample period was variable and coincided with an ongoing hydroacoustic fish stock assessment.

At each transect, we sampled three locations: river left (nearshore), river center (offshore), and river right (nearshore). Nearshore samples were collected approximately 20 m from shore, or at the closest distance at which total depth was great enough to accommodate a 5-m deep tow. At each location, we sampled at 0.5 m, 5 m, and 0.75 of the total depth during daytime and nighttime hours. Daytime was defined as 0.5 hr after sunrise to 0.5 hr before sunset, and nighttime was defined as 0.5 hr after sunset to 0.5 hr before sunrise. No tows were performed during the 1 hr periods encompassing sunrise and sunset. Using this strategy, a total of 18 samples were collected at each transect. This allowed us to compare cross-sectional location, depth, and diel variations in zooplankton abundance. In 1995 and 1996, the river-center sampling location was moved to correspond to the deepest point in the thalweg, and the 5-m deep tow was changed to a 3-m deep tow. These adjustments allowed us to better sample deep-water and near-shore areas within the reservoir cross section.

Physical habitat data were collected for correlation with zooplankton abundance in each reservoir. We deployed a bathythermograph at the river center location of each zooplankton sampling transect to obtain a vertical temperature profile of the water column directly after every zooplankton sampling transect. Hourly flow data for McNary and John Day dams were obtained from the Fish Passage Center (2005). The Pacific States Marine Fisheries Commission collected juvenile American shad passage data at John Day Dam through the Smolt Monitoring Program. Adult American shad dam passage data was collected by the U.S. Army Corps of Engineers (University of Washington 2005).

Juvenile American shad were also collected from August to November in John Day reservoir with a 12 m long monofilament mesh trawl with a 4.6 m² opening. The trawl was towed upstream and parallel to shore for 10 min to cover a distance of about 2,300 m. All fish were collected from the main-stem Columbia River during daylight hours in a 5-km section of the Columbia River downstream of Arlington, Oregon (rkm 382-387). We chose these sampling transects because they encompassed the area of a hydroacoustic assessment of juvenile American shad. We also collected juvenile American shad at night to verify that the abundances and composition of prey items

consumed did not vary from those we collected during the day. Fish were measured to the nearest millimeter fork length, immediately frozen with liquid nitrogen, and then stored at -80°C prior to analysis.

Sample Processing

In the laboratory, zooplankton samples were rinsed of formalin and diluted to an abundance of at least 40 organisms per ml (Cassie 1971). Three 1-ml aliquots were removed and zooplankton were counted with the aid of a compound microscope. A Folsom Splitter was used to split samples with diluted volumes greater than 4,000 ml. A total count (no aliquot subsampling) was used for samples with volumes less than 20 ml. Cladocerans other than *Daphnia* were identified to genus. *Daphnia* were identified to species, categorized as male, female, or ovigerous female, and measured to the nearest 0.01 mm. Measurements were made from the tip of the head to the posterior end of the carapace (excluding tail spine) using an ocular micrometer mounted in the compound microscope. Taxonomic identification followed Edmondson (1959) and Pennak (1989).

Juvenile American shad gut contents were analyzed for prey species composition and abundance from ten stomachs collected during each zooplankton sampling period. All prey items were counted, except where the total number of prey items exceeded 800 individuals. In these instances, we diluted the stomach contents to a known volume, extracted three 1-ml aliquots, and counted each taxon for each aliquot. Abundance was estimated for each taxon by multiplying the mean of the three 1-ml counts by the dilution factor.

Data Analysis

The mean of the three 1-ml counts for each taxonomic classification was multiplied by the dilution factor to provide a single estimate for each classification in each sample. Total zooplankton abundance used in statistical tests represented total organisms from the orders Cladocera, Branchiura, and Eucopepoda. Rotifer abundance data were not included in our analyses because the size of our mesh (153 μm) likely underestimated their abundance. Measurements of *Daphnia* were converted to biomass following the total length to weight regressions formulated by Culver et al. (1985) for

ovigerous and non-ovigerous forms of *Daphnia galeata mendotae* and *Daphnia retrocurva*. All other *Daphnia* species cumulatively represented less than 0.01% of all *Daphnia* collected in our study and were not included in biomass calculations.

Because of differences in general morphology, retention time, and seasonal sampling periods between the two reservoirs, we analyzed data from each reservoir separately. Zooplankton abundance (# m⁻³) and *Daphnia* biomass (µg m⁻³) were calculated for each sample. We evaluated the effects of river flow, water temperature, cross sectional location (nearshore or offshore), time of collection (day or night), and depth of collection on the abundance of crustacean zooplankton and *Daphnia* biomass in McNary and John Day reservoirs. For our analysis we pooled data across years (1994, 1995, and 1996) to increase the range of independent variables. We created a dummy variable for each of our two categorical variables (cross sectional location, diel classification). The reference level for cross sectional location was “nearshore” and the reference level for the diel variable was “daytime”. Some dependent variables were log₁₀ transformed before analysis to insure homoscedasticity (Zar 1999). Before conducting regression analysis, we calculated Pearson correlation coefficients (*r*) to examine the bivariate relation between all variables and to examine independent variables for collinearity. For regression model selection we used a forward selection technique, but then eliminated variables if their contribution (*R*²) to the final model was small.

For analysis of juvenile shad data, we used two-sample Wilcoxon rank sum tests to evaluate differences in median juvenile American shad abundance collected in trawls between years and one-way analysis of variance to compare juvenile American shad fork lengths between years. We also used two indices to examine prey diversity and selectivity of juvenile American shad. First, we used the Shannon-Weaver index (*H'*) to measure seasonal changes in the diversity of juvenile American shad prey items. The Shannon-Weaver index is defined as: $H' = -\sum p_i \log_{10} p_i$, where *p_i* is the proportion of prey items for individual taxa. This index is a measure of both the number of taxa and the frequency at which they occur. Second, we used a preference ranking described by Johnson (1980) to examine the seasonal change in prey preference in John Day Reservoir. Using this preference ranking method, the mean dif-

ference between the ranked availability and the ranked usage of prey items by juvenile American shad was tested for each sample period using a Waller-Duncan test.

Results

During our zooplankton sampling, daily river flows decreased to a minimum and water temperatures increased to a peak in mid to late summer in all years (Figure 2). During the three years of our study, seasonal patterns in river flow and water temperature were consistent, but there was substantial variation from year to year. For example, in 1994 in McNary Reservoir, river flows ranged from only 5,950 m³ s⁻¹ on June 1 to 2,739 m³ s⁻¹ on August 1. During the same period in 1996, river flows were much higher and ranged from 11,042 m³ s⁻¹ to 5,991 m³ s⁻¹. Conversely, water temperatures from June 1 to August 1 ranged from 13.9°C to 21.2°C in 1994 and from 12.7°C to 20.1°C in 1996. In 1995, river flows and water temperatures were generally intermediate to the low flows and high temperatures observed in 1994 and the high flows and low temperatures observed in 1996. Yearly trends in river flow and water temperature in John Day Reservoir were consistent with those observed in McNary Reservoir.

Vertical temperature profiles indicated no thermal stratification in either reservoir; however, stronger vertical temperature gradients were evident in 1994 when water temperatures were high and river flows were low. Over the three-year sampling period, we collected 167 vertical temperature profiles from McNary Reservoir and 56 from John Day Reservoir. Most profiles exhibited less than a 2°C difference between surface and bottom water temperatures in McNary Reservoir. The greatest variation in vertical temperature difference occurred in McNary Reservoir in 1994 when mean flows were the lowest of the three years. In that year, 66% of the profiles exhibited a greater than 2°C variation.

Community Structure and Size

We collected and analyzed 304 zooplankton samples from 35 sampling dates in McNary Reservoir and 530 samples from 54 dates in John Day Reservoir. Individual zooplankton sample abundance ranged from 21.8 to 30,650 m⁻³ in McNary Reservoir and from 24.4 to 68,856 m⁻³ in John Day Reservoir. The major zooplankton

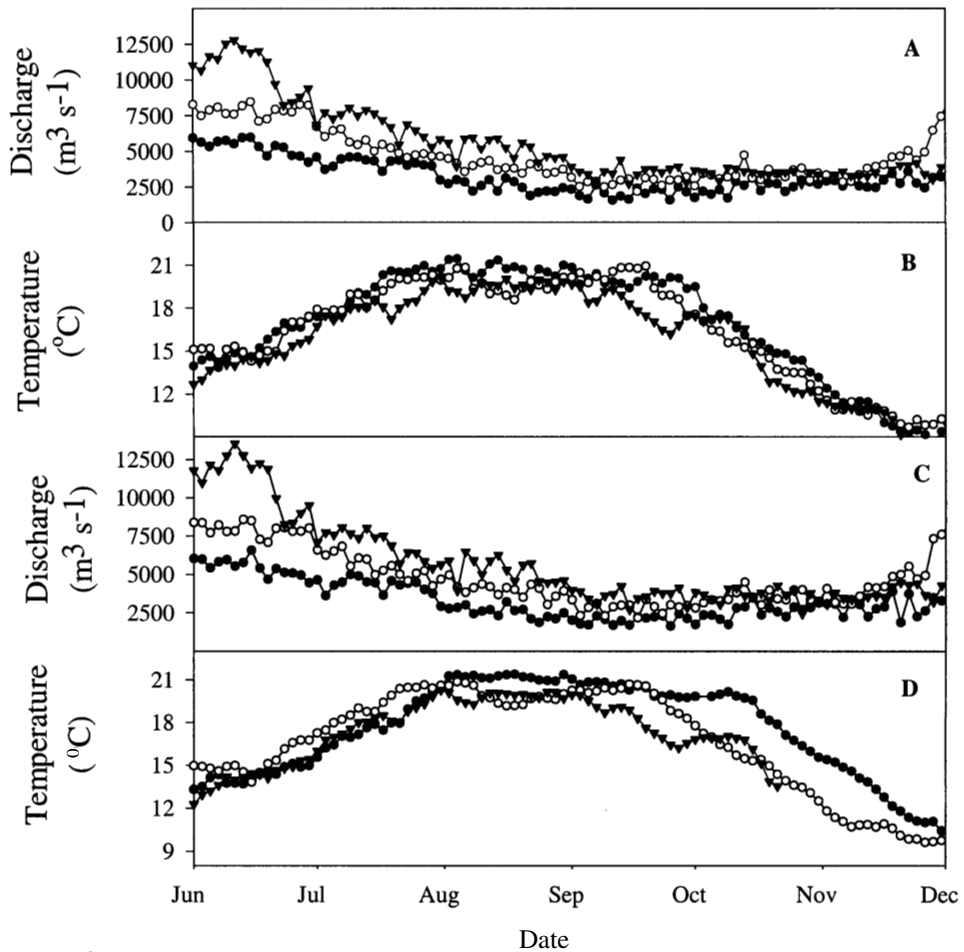


Figure 2. Seasonal changes in: A) mean daily discharge ($\text{m}^3 \text{s}^{-1}$) at McNary Dam, B) mean daily water temperature ($^{\circ}\text{C}$) at McNary Dam, C) mean daily discharge ($\text{m}^3 \text{s}^{-1}$) at John Day Dam, and D) mean daily water temperature ($^{\circ}\text{C}$) at John Day Dam. Solid circles, open circles, and triangles represent data collected in 1994, 1995, and 1996, respectively.

taxa collected in zooplankton net hauls were *Bosmina longirostris* (46%), cyclopoid copepods (22%), *Daphnia* (21%), and calanoid copepods (1%). Although our sampling design targeted crustacean zooplankton, we also encountered non-zooplankton taxa in our collections. We collected the mysid shrimp, *Neomysis mercedis* and the amphipod, *Corophium* in our samples, both of which are typically estuarine invertebrates. The mysid, *N. mercedis*, was present in 21% of night tows, but only 3% of day tows, with a maximum abundance of 54.2 m^{-3} . *Corophium* were only detected in small numbers. We also collected

small numbers of aquatic insects, predominately chironomid larvae (Table 1).

Seasonal patterns of *B. longirostris* and *Daphnia* abundances were generally consistent from year to year with high *Daphnia* abundance associated with low *B. longirostris* abundance in John Day Reservoir (Figure 3). Abundance of *B. longirostris* peaked in late June (1994) and July (1995, 1996) in McNary Reservoir and in early October (1994, 1995) in John Day Reservoir. No distinct *B. longirostris* peak was observed in John Day Reservoir in 1996. *Daphnia* abundance peaked in early August (all years) in John Day Reservoir; however, our

TABLE 1. Mean sample abundance (# m⁻³) of taxa collected at river km 381-514 of the Columbia River from June 1994 through October 1996. Standard errors of the means are shown in parentheses. The relative abundance of each taxon is shown as the percent of the total.

	McNary Reservoir	John Day Reservoir	Percent of Total
Phylum Annelida			
Class Oligochaeta	2.11(0.28)	0.19(0.08)	0.03
Class Polychaeta	<0.01(<0.01)	<0.01(<0.01)	<0.01
Phylum Arthropoda			
Class Arachnoidea	0.02(0.01)	<0.01(<0.01)	<0.01
Class Crustacea			
Order Amphipoda			
Family Corophiidae	0.16(0.07)	0.03(0.02)	<0.01
Family Gammaridae			
Family Gammarus spp.	<0.01(<0.01)	<0.01(<0.01)	<0.01
Order Cladocera			
Family Bosminidae			
Family Bosmina			
<i>Bosmina longirostris</i>	388.31(41.64)	2,654.72(301.58)	46.04
Family Chydoridae			
<i>Alona</i> spp.	25.71(3.83)	3.71(0.36)	0.45
<i>Chydorus</i> spp.	5.56(0.55)	10.62(1.11)	0.24
<i>Pleuroxus</i> spp.	0.71(0.18)	1.28(0.22)	0.03
<i>Leydigia quadrangularis</i>	2.02(0.53)	0.24(0.07)	0.03
<i>Campioereus rectirostris</i>	0.22(0.13)	0.08(0.05)	<0.01
<i>Eurycerus lamellatus</i>	0.04(0.02)	<0.01(<0.01)	<0.01
<i>Monospilus dispar</i>	0.34(0.08)	0.85(0.16)	0.02
Family Daphnidae			
<i>Ceriodaphnia</i> spp.	12.53(2.15)	8.68(1.00)	0.32
<i>Daphnia galeata mendotae</i>	130.35(57.02)	489.80(114.76)	9.38
<i>Daphnia parvula</i>	0.49(0.13)	0.18(0.09)	0.01
<i>Daphnia pulex</i>	0.64(0.19)	0.02(0.01)	0.01
<i>Daphnia retrocurva</i>	114.23(29.27)	740.13(109.87)	12.93
<i>Daphnia rosea</i>	0.12(0.05)	0.23(0.23)	<0.01
<i>Daphnia schødleri</i>	0.10(0.06)	-	<0.01
<i>Daphnia</i> spp.	16.07(2.92)	43.36(9.40)	0.90
<i>Scapholeberis</i> spp.	0.23(0.08)	1.57(0.29)	0.03
<i>Moina</i> spp.	1.87(0.36)	1.66(0.44)	0.05

	McNary Reservoir	John Day Reservoir	Percent of Total
Family Leptodoridae			
<i>Leptodora kindtii</i>	2.42(0.42)	16.68(2.48)	0.29
Family Macrothricidae			
<i>Illyocryptus</i> spp.	0.61(0.14)	0.54(0.13)	0.02
<i>Macrothrix</i> spp.	0.02(0.01)	0.01(0.01)	<0.01
Family Sidiidae			
<i>Diaphanosoma</i> spp.	1.31(0.39)	0.98(0.23)	0.03
<i>Sida crystallina</i>	2.65(0.04)	2.68(0.39)	0.08
Order Branchiura			
Suborder Arguloidea	<0.01(<0.01)	<0.01(<0.01)	<0.01
Suborder Cyclopoidea	201.35(13.04)	1,281.72(91.72)	22.44
Suborder Harpacticoida	1.12(0.15)	0.68(0.14)	0.03
Order Eucopepoda			
Suborder Calanoida	26.62(2.51)	78.90(9.62)	1.60
Order Mysidacea			
Family Mysidae			
<i>Neomysis mercedis</i>	0.84(0.26)	0.26(0.07)	0.02
Order Podocopa	0.08(0.03)	0.04(0.03)	<0.01
Class Insecta			
Order Collembola	0.02(0.01)	-	<0.01
Order Diptera	1.60(0.26)	0.20(0.07)	0.03
Order Ephemeroptera	0.52(0.13)	-	0.01
Order Hemiptera	<0.01(<0.01)	-	<0.01
Order Homoptera	<0.01(<0.01)	<0.01(<0.01)	<0.01
Order Hymenoptera	0.03(0.02)	<0.01(<0.01)	<0.01
Order Odonata	0.01(0.01)	-	<0.01
Order Trichoptera	<0.01(<0.01)	-	<0.01
Phylum Coelenterata			
Class Hydrozoa			
Family Hydridae			
<i>Hydra</i> spp.	0.20(0.06)	-	<0.01
Phylum Nematoda	1.07(0.19)	0.60(0.20)	0.03
Phylum Tardigrada	0.56(0.12)	0.15(0.08)	0.01
<i>Daphnia</i> spp. abundance	289.78(90.50)	1,332.36(222.61)	20.66
Total zooplankton abundance	989.62(111.82)	5,572.98(424.30)	

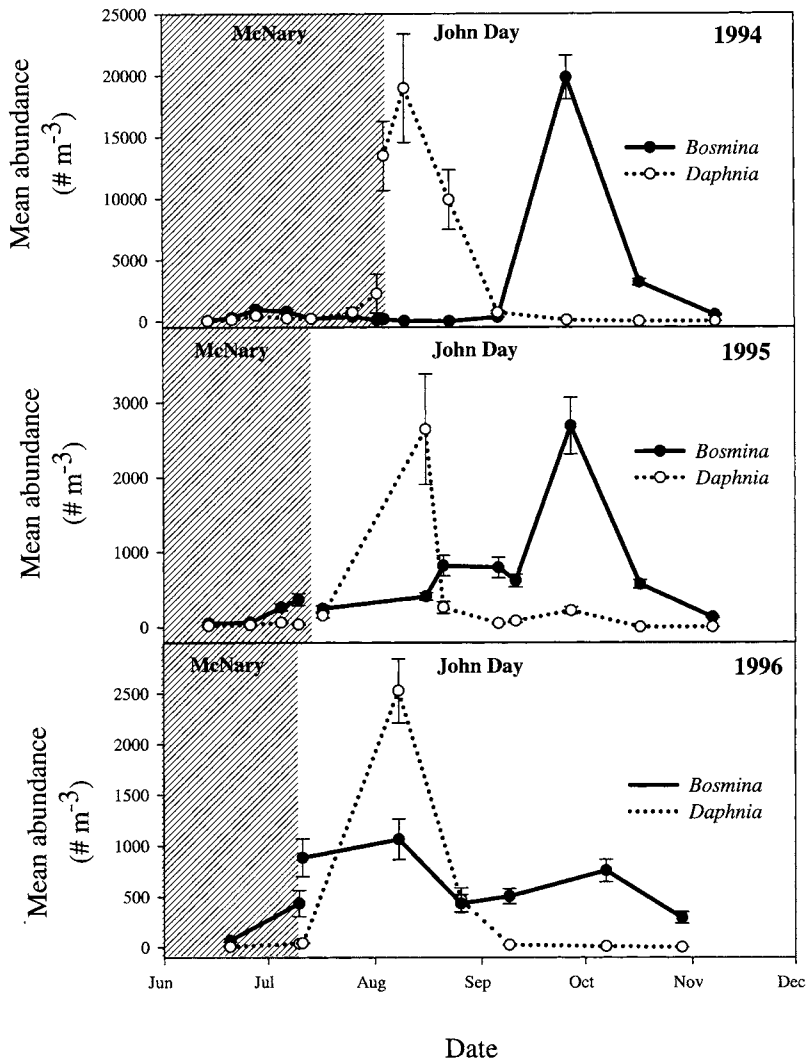


Figure 3. Seasonal changes in mean abundance of *Daphnia* and *Bosmina longirostris* in McNary and John Day reservoirs of the Columbia River, 1994-1996. McNary Reservoir and was sampled from June through July (shaded portion of the graph) and John Day Reservoir was sampled from August through November (unshaded portion of the graph). Sampling periods for reservoirs were timed to coincide with the outmigration of subyearling Chinook salmon.

sampling strategy did not allow us to determine the peak *Daphnia* seasonal abundance in McNary Reservoir. Seasonal peaks in *Daphnia* abundance in John Day Reservoir coincided with peak total zooplankton abundance and seasonal lows in *B. longirostris* abundance in 1994 and 1995. After a decline in *Daphnia* abundance in late August, we observed a rapid increase in *B. longirostris* abundance, which peaked in late September in

1994 and 1995. We did not observe this same *B. longirostris* response in 1996.

Mean *Daphnia* size in John Day Reservoir exhibited a dramatic reduction during September and October in all years (Table 2). Mean *Daphnia* size ranged from 0.54 to 0.98 mm in John Day Reservoir (individual size ranged from 0.3 to 2.2 mm) and from 0.70 to 1.04 mm in McNary Reservoir (individual size ranged from 0.4 to

TABLE 2. Sample period, mean length (mm), standard error (SE), and number (N) of *Daphnia* measured for each sampling period in McNary and John Day reservoirs.

Sample Period	Mean length (+SE)	Number (N)
<u>McNary Reservoir</u>		
<u>1994</u>		
6/14	0.90 (0.05)	95
6/21-6/23	0.95 (0.01)	491
6/28-6/30	0.92 (0.01)	1412
7/7	0.98 (0.02)	562
7/14	0.92 (0.01)	727
7/26-7/27	0.98 (0.01)	858
8/2-8/3	1.04 (0.01)	1241
<u>1995</u>		
6/14	0.79 (0.02)	190
6/26-6/28	0.83 (0.01)	399
7/5-7/7	0.83 (0.01)	933
7/10-7/11	0.81 (0.02)	309
<u>1996</u>		
6/20-6/25	0.72 (0.01)	445
7/10-7/11	0.76 (0.02)	319
7/22-7/25	0.99 (0.01)	721
8/29	0.82 (0.01)	473
10/9-10/10	0.85 (0.01)	412
<u>John Day Reservoir</u>		
<u>1994</u>		
8/4	0.87 (0.01)	767
8/10	0.92 (0.01)	1690
8/23-8/25	0.83 (0.01)	3148
9/6-9/9	0.70 (0.01)	1840
9/26-9/29	0.66 (0.01)	320
10/17-10/20	0.67 (0.04)	59
11/8-11/9	0.98 (0.04)	116
<u>1995</u>		
7/17-7/19	0.84 (0.01)	657
8/16	0.76 (0.01)	980
8/21-8/23	0.80 (0.01)	586
9/6-9/7	0.64 (0.02)	187
9/11-9/14	0.72(0.14)	304
9/27	0.60(0.01)	168
10/17-10/19	0.59 (0.02)	20
11/7	0.85 (0.02)	163
<u>1996</u>		
7/11-7/12	0.89 (0.02)	258
8/8	0.81 (0.01)	1606
8/26-8/29	0.71 (0.01)	715
9/9-9/10	0.70 (0.02)	148
10/7-10/9	0.69 (0.02)	117
10/29	0.63 (0.01)	80

2.3 mm). The timing of reduction in *Daphnia* size coincided with peak juvenile American shad numbers in John Day Reservoir in late summer (Figure 4B).

Temporal and Spatial Dynamics

Seasonal patterns in total zooplankton abundance and *Daphnia* biomass were similar for both reservoirs. Mean zooplankton sample period abundance ranged from 185 m⁻³ to 2,341 m⁻³ in McNary Reservoir (Figure 5A) and from 406 m⁻³ to 26,482 m⁻³ in John Day Reservoir (Figure 5B). Mean *Daphnia* biomass ranged from 8 µg m⁻³ to 80 µg m⁻³ in McNary Reservoir (Figure 5C) and from 2 µg m⁻³ to 118 µg m⁻³ in John Day Reservoir (Figure 5D). In McNary Reservoir, total zooplankton abundance and *Daphnia* biomass was greatest in early August. Peaks in early July coincided with the outmigration of subyearling Chinook salmon. Peaks in early August occurred at the end of the outmigration (Figure 4A). In John Day Reservoir, zooplankton abundance and *Daphnia* biomass peaked in mid to late August. This peak occurred after most of the subyearling Chinook salmon had emigrated from the reservoir (Figure 4B).

Our multiple regression models indicated that physical variables were more important in explaining variations in zooplankton abundance and *Daphnia* biomass than spatial variables. In John Day Reservoir, river flow and water temperature explained 56% of the variation in total zooplankton abundance, but only 8% of the variation in *Daphnia* biomass (Table 3). We left water temperature and river flow together in the same models for John Day Reservoir despite the fact that they exhibited minor collinearity ($r = -0.18$, $P < 0.001$). For total zooplankton abundance, diel classification and tow depth were both significant ($P < 0.05$); however, they only explained 1.3% of additional variation in zooplankton abundance. In McNary Reservoir, river flow explained most of the variation in zooplankton abundance and *Daphnia* biomass. Our final regression model for McNary Reservoir indicated a significant relationship between cross-sectional location and zooplankton abundance and that littoral zooplankton abundance was greater than limnetic zooplankton abundance. No spatial variables remained in the final regression models for zooplankton abundance or *Daphnia* biomass in John Day Reservoir.

Seasonal abundance increases of all the major zooplankton taxa were associated with increases

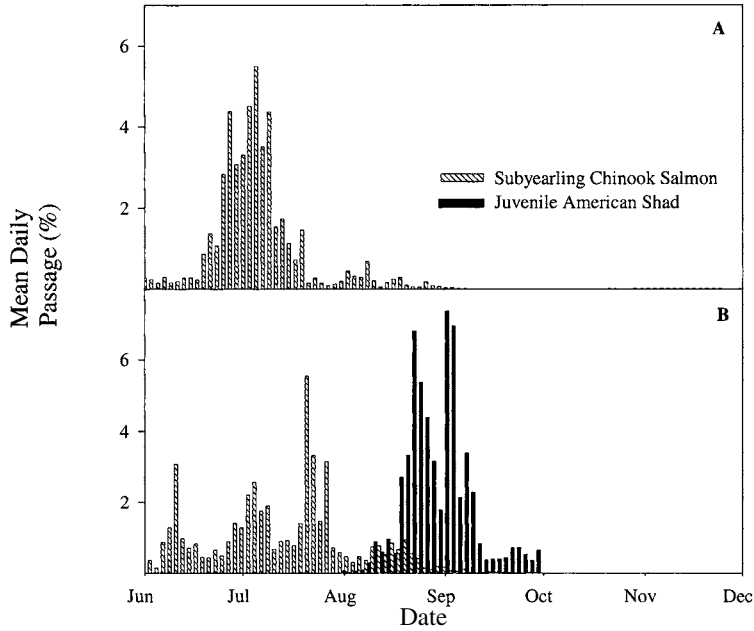


Figure 4. Seasonal changes in A) mean daily percent subyearling Chinook salmon passage from McNary Dam, and B) mean daily percent subyearling Chinook salmon and juvenile American shad passage from John Day Dam, Columbia River, 1994-1996. Juvenile American shad data were not available for McNary Dam.

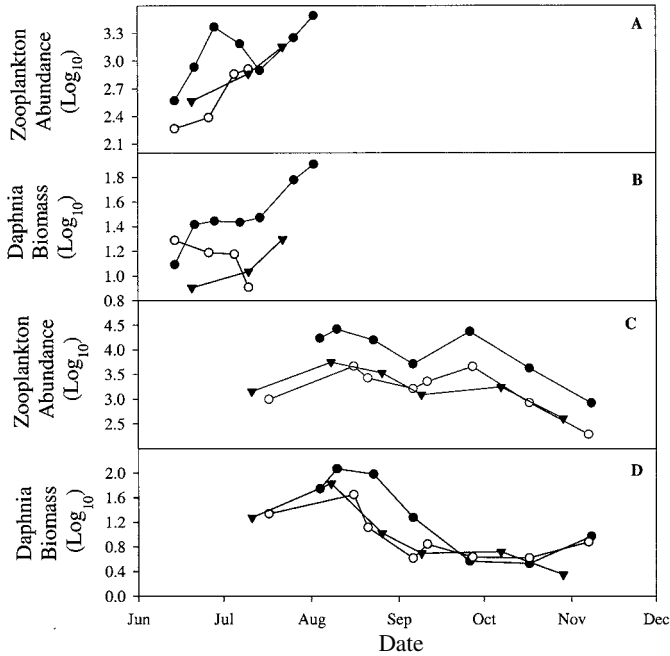


Figure 5. Seasonal changes in: A) \log_{10} mean zooplankton abundance ($\# \text{ m}^{-3}$), from McNary Reservoir, B) \log_{10} mean *Daphnia* biomass ($\mu\text{g m}^{-3}$) from McNary Reservoir, C) \log_{10} mean zooplankton abundance ($\# \text{ m}^{-3}$), from John Day Reservoir, and D) \log_{10} mean *Daphnia* biomass ($\mu\text{g m}^{-3}$) from John Day Reservoir of the Columbia River. Solid circles, open circles, and triangles represent data collected in 1994, 1995, and 1996, respectively.

TABLE 3. Best fit multivariate and bivariate regression results for total zooplankton abundance (# m⁻³) and *Daphnia* biomass (µg m⁻³) collected from McNary and John Day reservoirs, 1994-1996. Factors include mean daily flow (m³ s⁻¹) and water temperature (°C) collected at McNary and John Day dams, and cross sectional location (onshore vs. offshore) of zooplankton collection.

Factor	Regression coefficient (b)	SE	t-value (b=0)	Prob. (b=0)	R ²	P
<u>McNary Reservoir</u>						
<u>Zooplankton abundance</u> ¹						
Constant	3.310	0.077	43.26	<0.001	0.183	<0.001
Flow	<-0.001	<0.001	-5.68	<0.001		
X-Sectional Location	-0.231	0.046	-5.04	<0.001		
<u><i>Daphnia</i> biomass</u>						
Constant	338.012	38.056	8.88	<0.001	0.158	<0.001
Flow ¹	-85.117	10.113	-8.42	<0.001		
<u>John Day Reservoir</u>						
<u>Zooplankton abundance</u> ¹						
Constant	5.103	0.475	10.74	<0.001	0.562	<0.001
Flow ¹	-1.226	0.125	-9.79	<0.001		
Temperature	0.140	0.145	21.57	<0.001		
<u><i>Daphnia</i> biomass</u> ¹						
Constant	1.384	0.759	1.82	0.069	0.082	<0.001
Temperature	0.068	0.015	4.53	<0.001		
Flow ¹	-0.524	0.178	-2.94	0.004		

¹Log₁₀ transformed variable

in water temperature and decreases in discharge in both reservoirs. In McNary Reservoir, *Daphnia* abundance was the taxa most highly correlated with water temperature ($r = 0.19$) and discharge ($r = -0.18$). In John Day Reservoir, cyclopoid copepod abundance was the taxa most highly correlated with water temperature ($r = 0.41$) and discharge ($r = -0.27$) (Table 4).

Juvenile Shad

During our three years of trawling in John Day Reservoir, we collected 21,637 juvenile American shad from 205 trawls. Shad comprised over 98% of all fish captured in this study, and we only captured 161 subyearling Chinook salmon. Median and maximum juvenile American shad abundances were 0.95 fish per 1,000 m³ and 92.3 fish per 1,000 m³, respectively.

Trawl catches were significantly higher in 1995 (median = 2.81 fish per 1,000 m³) than in 1994 (median = 0.72, $Z = -4.74$, $P < 0.001$) and 1996 (median = 0.40, $Z = -4.86$, $P < 0.001$). In 1995, we observed peak catches in late August and lower catches in late September and late October, but no seasonal trends in abundance were evident in

1994 and 1996 (Figure 6A). Juvenile American shad were significantly larger in 1994 ($F = 156.2$, $P < 0.001$) than in 1995 (difference in means = 10.3 mm) and 1996 (difference in means = 11.2 mm) (Figure 6B). Passage data at John Day Dam showed the greatest number of juvenile American shad emigrated from the reservoir from mid August

TABLE 4. Pearson correlation coefficients (r) of major zooplankton taxa with temperature and discharge in McNary and John Day reservoirs of the Columbia River.

Parameter	Temperature	Discharge
<u>McNary Reservoir</u>		
Zooplankton abundance	0.20	-0.23
<i>Daphnia</i> abundance	0.19	-0.18
<i>Bosmina longirostris</i> abundance	0.06	-0.11
Cyclopoid copepod abundance	0.15	-0.16
Calanoid copepod abundance	0.07	-0.20
<u>John Day Reservoir</u>		
Zooplankton abundance	0.35	-0.31
<i>Daphnia</i> abundance	0.25	-0.12
<i>Bosmina longirostris</i> abundance	0.16	-0.27
Cyclopoid copepod abundance	0.41	-0.27
Calanoid copepod abundance	0.19	-0.08

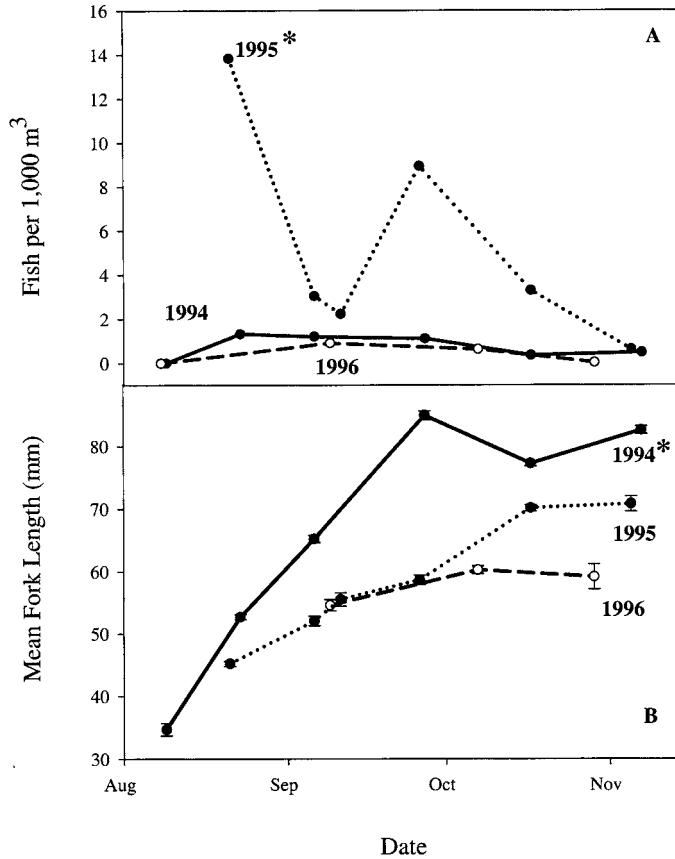


Figure 6. Seasonal changes in: A) median abundance, and B) mean (\pm SE) fork length of juvenile American shad, collected by mid-water trawl in John Day Reservoir, Columbia River, 1994-1996. * Denotes a significant difference between years.

to mid September with peak passage occurring in early September (Figure 4B). Although juvenile American shad counts were discontinued at John Day Dam in late October, trawling data indicated that shad were present in John Day Reservoir at least into November with a median trawl abundance of 0.55 fish per 1,000 m³.

Juvenile American shad collected from John Day Reservoir were planktivorous, with zooplankton taxa representing over 99% of their diet. Overall, the most abundant taxa in the diet of juvenile American shad were cyclopoid copepods, *Daphnia*, *B. longirostris*, and *Leptodora kindtii*, respectively. Non-zooplankton taxa collectively represented less than 0.5% of total prey items consumed by juvenile American shad in each

sample period except in early November. Non-zooplankton taxa were *N. mercedis*, the Asian clam, *Corbicula fluminea*, *Corophium*, and Dipterans. Diet composition did not differ between the day and night in 1994, but abundance of prey in stomachs of fish collected at night was less than during the day in 1995.

When the seasonal abundance of zooplankton was low in October and November, small (1-2 mm) *C. fluminea* represented 9% and 25% of the total prey items consumed in 1994 and 1995, respectively. Although *B. longirostris* represented a higher numerical proportion of the diet in November (86% in 1994, 63% in 1995), a single *C. fluminea* larva is many times heavier by weight and has a higher energetic importance

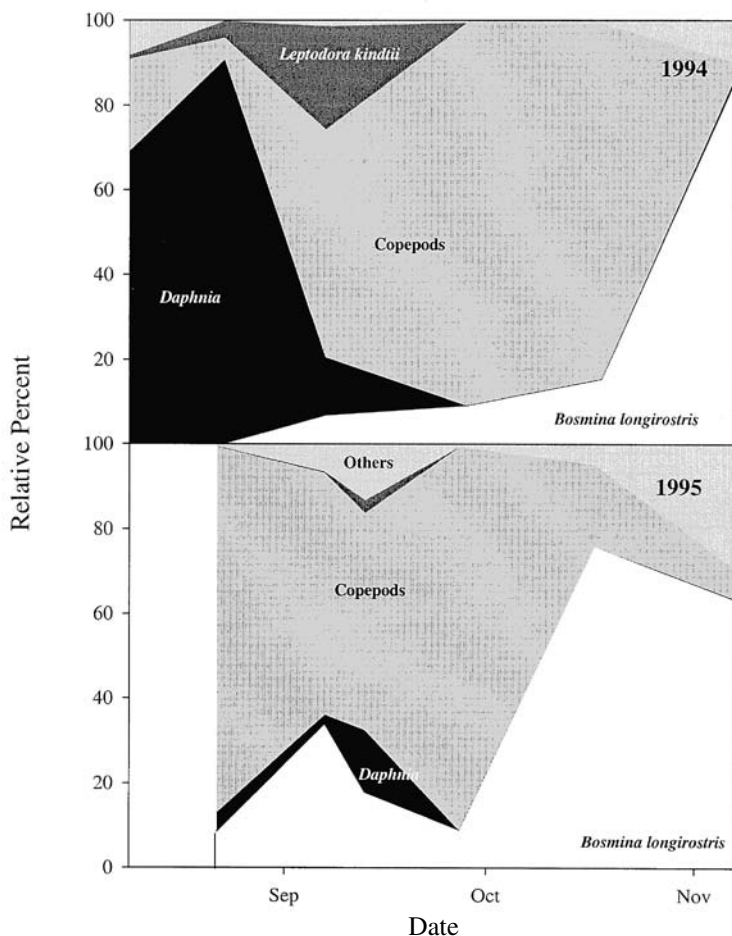


Figure 7. Relative percentage of prey items identified in stomachs from American shad juveniles collected in John Day Reservoir, Columbia River, in 1994 and 1995.

to an individual fish. Seasonal variations in diet were evident in both 1994 and 1995 (Figure 7). Smaller juvenile American shad primarily fed on *Daphnia* in August, but switched to more evasive copepods as the mean size of fish increased. This was particularly evident in 1994. This switch in diet accompanied the decline in *Daphnia* abundance in August and the increase in *B. longirostris* abundance in September. By early November, the diet of juvenile shad consisted primarily of *B. longirostris* and *C. fluminea*.

The diet of juvenile shad was the most diverse in early to mid September during both years (Figure 8). Diversity values ranged from 0.15 to 0.61, with a possible diversity range of 0 (low diversity) to 1.34 (high diversity) based on the total number

of taxa (21) we collected from juvenile shad stomachs. During both years, low diversity values corresponded with the dominance of *Daphnia* and copepods in shad diets. In early September 1994, high diversity corresponded with the transition in dominant prey items from *Daphnia* to copepods. Despite having a smaller percentage of *Daphnia* in 1995, seasonal trends in prey item diversity were similar to those from 1994.

Despite being the most numerous prey items in juvenile shad stomachs, *Daphnia*, cyclopoid copepods, and *B. longirostris* were not the most preferred (Table 5). Our rank of preference analysis revealed that juvenile American shad preferentially preyed on calanoid copepods and *L. kindtii* during most sample periods in 1994, although these

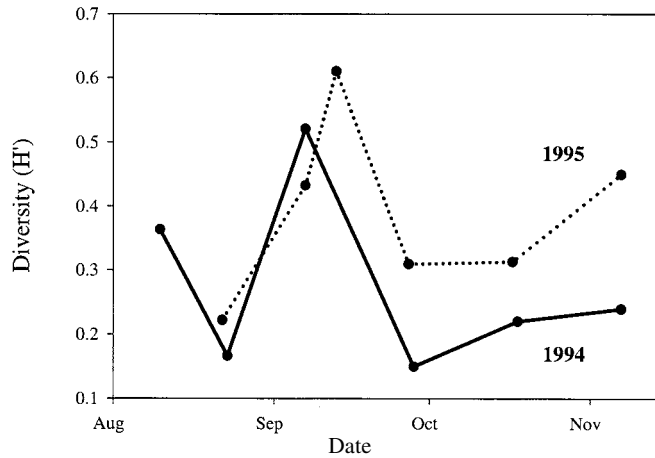


Figure 8. Seasonal change in juvenile American shad prey item diversity collected in John Day Reservoir, Columbia River, 1994 and 1995. Diversity values were calculated using the Shannon-Weaver index (H').

TABLE 5. Prey preference ranks (1=most preferred) of juvenile American shad collected from John Day Reservoir, Columbia River. For each date, taxa with the same letters were not significantly different from each other using the Waller-Duncan K-ratio T test. Taxa abbreviations are: Alo=*Alona* spp., Arg=*Arguloida*, Bom=*Bosmina longirostris*, Cal=*Calanoida*, Cer=*Ceriodaphnia* spp., Chy=*Chydorus* spp., Cob=*Corbicula fluminea*, Cor=*Corophium* spp., Cyc=*Cyclopoida*, Dap=*Daphnia* spp., Dip=*Dipteran*, Har=*Harpacticoida*, Hom=*Homoptera*, Hym=*Hymenoptera*, Ily=*Ilyocryptus* spp., Lep=*Leptodora kindtii*, Ley=*Leydigia quadrangularis*, Mon=*Monospilus dispar*, Neo=*Neomysis mercedis*, Ost=*Ostracoda*, and Sid=*Sida crystallina*.

Date	Rank of preference													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<u>1994</u>														
8/10	Cal (a)	Lep (b)	Cyc (b)	Dap (b)	Dip (b)									
8/23	Lep (a)	Cal (b)	Bom (c,b)	Har (c,d)	Cyc (e,d)	Sid (e)	Dap (f)							
9/07	Lep (a)	Dap (b)	Cal (c,b)	Bom (c,b,d)	Cyc (c,d)	Har (d)	Ley (d)							
9/28	Cer (a)	Cal (b)	Arg (c,b)	Lep (c,b,d)	Dap (c,b,d)	Lep (c,b,d)	Bom (c,b,d)	Cyc (c,d)	Alo (c,d)	Chy (d)				
10/18	Cal (a)	Cer (b)	Har (c,b)	Dap (c,b)	Alo (c,b)	Chy (c,d)	Lep (c,d)	Ley (c,d)	Cyc (d)	Bom (d)				
11/07	Cob (a)	Bom (b)	Cyc (c,b)	Arg (c,b)	Dip (c,b)	Cal (c,b)	Chy (c,d)	Sid (e,d)	Alo (e,d)	Dap (e)				
<u>1995</u>														
9/07	Ily (a)	Alo (b)	Bom (c,b)	Lep (c,b)	Dap (c,b,d)	Cob (c,b,d)	Cal (c,d)	Cyc (d)	Mon (d)	Sid (d)				
9/13	Alo (a)	Ily (b,a)	Cal (b,c)	Bom (b,c,d)	Lep (e,c,d)	Sid (e,f,c,d)	Cob (e,f,d)	Cor (e,f,d)	Neo (e,f,d)	Ost (e,f)	Cer (e,f)	Cyc (e,f)	Mon (f)	Dap (f)
9/27	Alo (a)	Lep (a)	Dap (a)	Cal (a)	Dip (a)	Cob (a)	Cyc (a)	Bom (a)						
10/17	Alo (a)	Cob (a)	Cal (a)	Bom (a)	Cor (a)	Cyc (a)	Har (a)	Ost (a)	Lep (a)					
11/07	Cob (a)	Bom (b)	Cor (b)	Cal (c,b)	Cyc (c,b)	Sid (c,d)	Hom (e,d)	Hym (e,d)	Alo (e)					

taxa were not major food items of juvenile shad. During 1995, *Alona* spp. exhibited the highest or second highest preferential rank in September and October; however, mean differences between it and other taxa were not significant ($P > 0.05$). *C. fluminea* was the most preferred prey item in early November for both years (rank of preference = 1, $P < 0.05$).

Discussion

The composition of cladoceran zooplankton taxa in our study was similar to that described for McNary Reservoir (Scarola 1968) and the Hanford Reach of the Columbia River (Neitzel et al. 1982). However, we did collect some previously unreported taxa. We collected *Camptocercus rectirostris* and *Moina* spp. in our study and found no mention by others of their presence in the lower Snake or Columbia rivers. In our study, we found six species of *Daphnia*, the most abundant of which were *D. retrocurva* and *D. galeata mendotae*. Both of these species are common in the Columbia River (Scarola 1968; Rondorf et al. 1990). Less abundant *Daphnia* were *Daphnia rosea*, which was reported in the upper Columbia River by Beckman et al. (1985), and *Daphnia pulex*, *Daphnia parvula*, and *Daphnia schødleri*, which are also found in the lower Snake River (Harris 1979). We did not document the presence of *Daphnia middendorffiana* as did Neitzel et al. (1982) in the Hanford Reach. This may be due to the seasonal differences in *Daphnia* morphology and hybridization between species (Pennak 1989).

The abundance of *B. longirostris* is usually controlled by the abundance of flagellated algae, whereas *Daphnia* abundance is more influenced by predation because of their larger body size. *B. longirostris* abundance in lakes typically is bimodal with peaks in early summer and early autumn; however, *Daphnia* generally remains abundant from June through October (Demott 1989). The *Daphnia* species available to subyearling Chinook salmon and juvenile American shad in our study area were *D. galeata mendotae* and *D. retrocurva*. The primary *Daphnia* species in our study, *D. retrocurva*, typically has one seasonal maximum when water temperature exceeds 20°C, while *D. galeata mendotae* has two seasonal maxima (Wetzel 2001). The seasonal trends exhibited by *B. longirostris* were similar to other studies; however, the collapse of *Daphnia* in early August is indicative of heavy planktivory by shad.

In both reservoirs, we collected *Corophium* and *N. mercedis* that are typically estuarine, but have become established in Columbia and Snake river reservoirs. *Corophium salmonis* and *Corophium spinicorne* are important food resources of juvenile salmonids in Lower Granite Reservoir of the Snake River (Muir and Coley 1996), the Bonneville Pool (Muir and Emmett 1988), and the lower Columbia River (Kirn et al. 1986). Unlike *Corophium*, *N. mercedis* is not an important food source of juvenile salmonids and may be largely unavailable as prey due to its diel migration within the water column. Mysids have had large-scale impacts on food webs in other systems and also prey on *Daphnia* in John Day Reservoir (Haskell 2003).

Our analysis indicated that spatial factors explained little of the variation in zooplankton population dynamics. This was due to both the physical characteristics of our study reservoirs and the fact that our sampling did not adequately capture the variability present. Yearly differences in water temperature and flow consistently explained the greatest percentage of variation in zooplankton parameters. In 1994, zooplankton abundance, *Daphnia* biomass, and *Daphnia* size were greater than in 1995 or 1996 and were associated with higher water temperature and lower river flow.

Zooplankton populations in large riverine reservoirs are strongly influenced by physical factors. The controlling factor that structures zooplankton communities in the main-stem Columbia River is reservoir retention time. We found zooplankton abundance to be 5-10 times greater in John Day Reservoir where the retention time is about twice that of McNary Reservoir. Columbia River reservoirs are operated as run-of-the-river and are characterized by relatively high velocities and low retention times. This explains the lack of thermal stratification and cross-sectional variation we observed. Only in low-flow years, such as in 1994, did the potential exist for warming of the upper water column due to surface warming. Riverine reservoirs with short retention times generally favor smaller-bodied zooplankton taxa with short generation times (Pace et al. 1992). The dominant taxa in our study of McNary and John Day reservoirs were *Bosmina*, copepods, rotifers, and smaller *Daphnia*. These taxa are the same as those from other rivers with low retention times such as the Orinoco River, Venezuela (Saunders and Lewis 1989), the Ohio River, Kentucky (Thorp

et al. 1994), and the Hudson River, New York (Pace et al. 1992).

We observed greater crustacean zooplankton abundance in littoral habitats than in limnetic habitats in McNary Reservoir and attribute the relation to higher retention of zooplankton in low-velocity habitats. The Ohio River exhibited greater abundances of cladocerans and copepods in littoral areas during the summer relative to limnetic areas (Thorpe et al. 1994). High winds, seasonally common to our study area in John Day Reservoir, may create enough turbulence to further mix the water and decrease littoral abundance (Marzolf 1990). The lack of cross-sectional variation of zooplankton abundance in John Day Reservoir is somewhat attributable to our study design because we did not sample in water less than 5 m in depth (3 m depth in 1995 and 1996). We also did not sample backwater populations that exhibit greater abundance than mainstem sampling locations in John Day Reservoir (Haskell 2003).

In the upper reaches of rivers, water velocity is generally too high to allow zooplankton to become established in the main channel, because zooplankton loss due to downstream transport typically exceeds production in a given area (Hynes 1970). Decreased flows and sedimentation in backwater areas allow zooplankton communities to establish, which can be advected into the main channel. This phenomenon may allow the establishment of populations of zooplankton in the mainstem Columbia River. Alternatively, Saunders and Lewis (1989) found significant downstream increases in copepod and *Bosmina* abundance in mainstem habitats that could not be attributed to tributary inputs and transitory reproduction in the Orinoco River, Venezuela. This indicated zooplankton originated from areas within the mainstem. It may be possible for downstream increases in zooplankton to occur above and beyond tributary or backwater inputs. We believe that mainstem zooplankton abundance in McNary and John Day reservoirs is determined by both advection from backwater areas and by mainstem production.

Juvenile shad are mostly planktivorous in John Day Reservoir and preferentially select the largest bodied zooplankton. Of the major zooplankton taxa we collected in net hauls, *Daphnia* were the most abundant, large zooplankton and therefore were highly utilized by sight feeding juvenile shad. Diversity of the juvenile shad prey assemblage

was low when *Daphnia* were the primary prey item and again in late September when cyclopoid copepods were the primary prey item. In 1994, *L. kindtii* and calanoid copepods were more preferred prey of juvenile shad because of their relatively large size; however, their abundance in our study was low. *L. kindtii* is the largest of all the cladocera, with a size range of 7-18 mm, and calanoid copepod genera are all relatively large with adults in excess of 1 mm.

Yearly variability in water temperature and discharge influences the number of *Daphnia* available in the Columbia River and the seasonal peak in *Daphnia* coincides with the transition of larval shad into juveniles. *Daphnia* size and abundance peaked in early August as water temperatures neared their peak and flows were low. At this time juvenile American shad were increasing in abundance. We observed a reduction in cladoceran body size, which can be an indication of size selective planktivory (Brooks and Dodson 1965). In our study, juvenile American shad were the most abundant fish collected in mid-water trawls during August and September, and second only to cottids as larvae from June to August (Gadomski and Barfoot 1998). We believe juvenile American shad play an important role in the decline in *Daphnia* abundance and size during August and September.

American shad larval abundance in the Columbia River mainstem peaks in July, but declines by early August as larval fish transition to the juvenile phase (Petersen et al. 2003). The timing of this transition coincides with the dominance of *Daphnia* in shad stomach contents and peak *Daphnia* abundance from net hauls in early August. Year class strength of American shad is likely determined by the availability of *Daphnia* during this transition period. This is important because American shad year class strength in the Connecticut River is determined by the survival of fish in the larval phase (Crecco et al. 1983). After the disappearance of *Daphnia* in John Day Reservoir by late August, juvenile shad switch to more abundant cyclopoid copepods. By this time increased body size likely allows juvenile American shad to exploit more evasive copepods. The seasonal shift in American shad prey items is consistent with changes we observed in the zooplankton community.

Our data indicates that juvenile shad persist in John Day Reservoir at least into November

when zooplankton biomass is low, preferentially feeding on introduced *C. fluminea* clam larvae. *C. fluminea* larvae are free living in the water column and the majority of larvae are released in late fall (Pennak 1989), which coincides with later migrating juvenile shad presence in John Day Reservoir. In the Columbia River estuary, *C. fluminea* is one of the most dominant benthic invertebrates (McCabe et al. 1997; McCabe et al. 1998) and in the spring and summer American shad utilize it as a primary food source (McCabe et al. 1983). *C. fluminea*, was first discovered in the United States in the Columbia River in 1938, yet little is known of the function of *C. fluminea* in Columbia River food webs.

The seasonal disappearance of *Daphnia* in John Day Reservoir is potentially deleterious for stocks of subyearling Chinook salmon listed under the Endangered Species Act (ESA) because *Daphnia* are a major food item in reservoir habitats (Rondorf et al. 1990) and numbers of American shad in John Day Reservoir are increasing. Data collection by Rondorf et al. (1990) occurred in McNary Reservoir, the next reservoir upstream from John Day Reservoir, during 1980-1982. The number of adult American shad returning to

McNary Reservoir increased 123% from 1980 to 1994 (the beginning of this study), and increased 143% from 1994 to 2004. Therefore, it is likely that if juvenile shad prey on the same food items in McNary Reservoir as they do in John Day Reservoir, the use of *Daphnia* prey by subyearling Chinook salmon as a food source has been increasingly disrupted. Later-migrating ESA-listed Snake River subyearling Chinook salmon could be affected by *Daphnia* declines because they migrate through McNary and John Day reservoirs in August (William Connor, U.S. Fish and Wildlife Service, unpublished data) when juvenile shad are abundant and feeding on zooplankton.

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