

Feeding Ecology of Larval Fishes in Lake Roosevelt, Washington

Abstract

Food habits, feeding selectivity, and diet overlap were analyzed for larval walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), sculpins (*Cottus spp.*), and suckers (*Catostomus spp.*) collected in Lake Roosevelt, Washington, in May to July 1982. Larval diet of fishes in this unique co-occurring species mix has not been previously described. Larval fishes 4-25 mm long were sampled weekly with 0.5-m townets from nearshore sites at two stations. Zooplankton was collected with Miller samplers to characterize food availability. The most abundant food items were calanoid copepods in walleye stomachs, calanoid and cyclopoid copepods in yellow perch stomachs, and cyclopoid copepods in sculpin stomachs. Larval walleyes 9 to 24 mm long also preyed upon larval fishes. Cladocerans were important food only to larval suckers, which fed almost exclusively on *Bosmina* and *Chydorus*. Feeding selectivity, determined by Wilcoxon's nonparametric signed-rank analysis, showed positive selection for several prey items among the fish taxa. Schoener's niche overlap values indicated significant diet overlap between walleye and yellow perch. During our study period, effects of competition on growth, survival, and character divergence of larval walleye and yellow perch was minor. Annual variation in reservoir conditions could result in stronger or weaker competitive interactions than we observed since zooplankton composition is known to influence fry feeding success and growth.

Introduction

The transition of larval fish from endogenous to exogenous feeders results in a "critical period" (Bagnal 1978) when availability of suitable prey has important effects on survival. The initial strength and ultimate success of percid year classes are usually determined during the first year of life, therefore the description of factors that can affect year class characteristics is important in the management of percid fisheries (Maloney and Johnson 1957; Forney 1976, 1980; MacLean and Magnuson 1977; Sems 1987). Although diet of coexisting larval walleye and yellow perch has been described for other areas (Maloney and Johnson 1957, Smith and Pycha 1960, Bulkley *et al.* 1976, Keast 1979), it has not been reported from the Columbia River system, which supports the largescale (*Catostomus macrocheilus*) and bridgelip (*C. columbianus*) suckers and the prickly sculpin (*Cottus asper*) which are not found elsewhere in the range of these percids.

We documented food habits of coexisting larval walleye, yellow perch, sculpins, and suckers in Lake Roosevelt. Zooplankton consumption by larval fishes was compared to abundance of zooplankton in the water, and prey selectivity was evaluated. We considered diet overlap in conjunction with prey availability and selection data to de-

scribe potential competitive interaction in the larval fish assemblage.

We expected diets of larval percids in Lake Roosevelt would be dissimilar to those reported from other systems, with the difference attributable to regional prey availability and potential competitive interactions resulting from diet overlap with unique co-occurring species.

Study Area

Lake Roosevelt, the largest lake in Washington, includes that portion of the Columbia River and its tributaries impounded by Grand Coulee Dam (Figure 1). The reservoir is 243 km long, has a surface area of 33,490 ha, a maximum depth of 122 m, and a maximum width of 3.4 km. Stober *et al.* (1980) provided a detailed account of the limnology, geography, and climate of the lake and surrounding area.

Walleye and yellow perch, believed to have been introduced into the Columbia River system in the late 1940s (Bregé 1981), were first reported in Lake Roosevelt in the early 1960s (Fletcher 1987). The walleye has become an important sport fish in the lake, adding 1.5 to 2.5 million dollars annually to the local economy (Beckman *et al.* 1985). Porcupine Bay, located in the Spokane River arm of the reservoir, is reported to have the highest sport fishery harvest rates of walleye in Washington (Fletcher 1987). This economic significance, the popularity and success of angling for walleye, and a lack of fishery-related information

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³The Unit is jointly supported by the U.S. Fish and Wildlife Service, Montana Dept. of Fish, Wildlife and Parks and Montana State University.

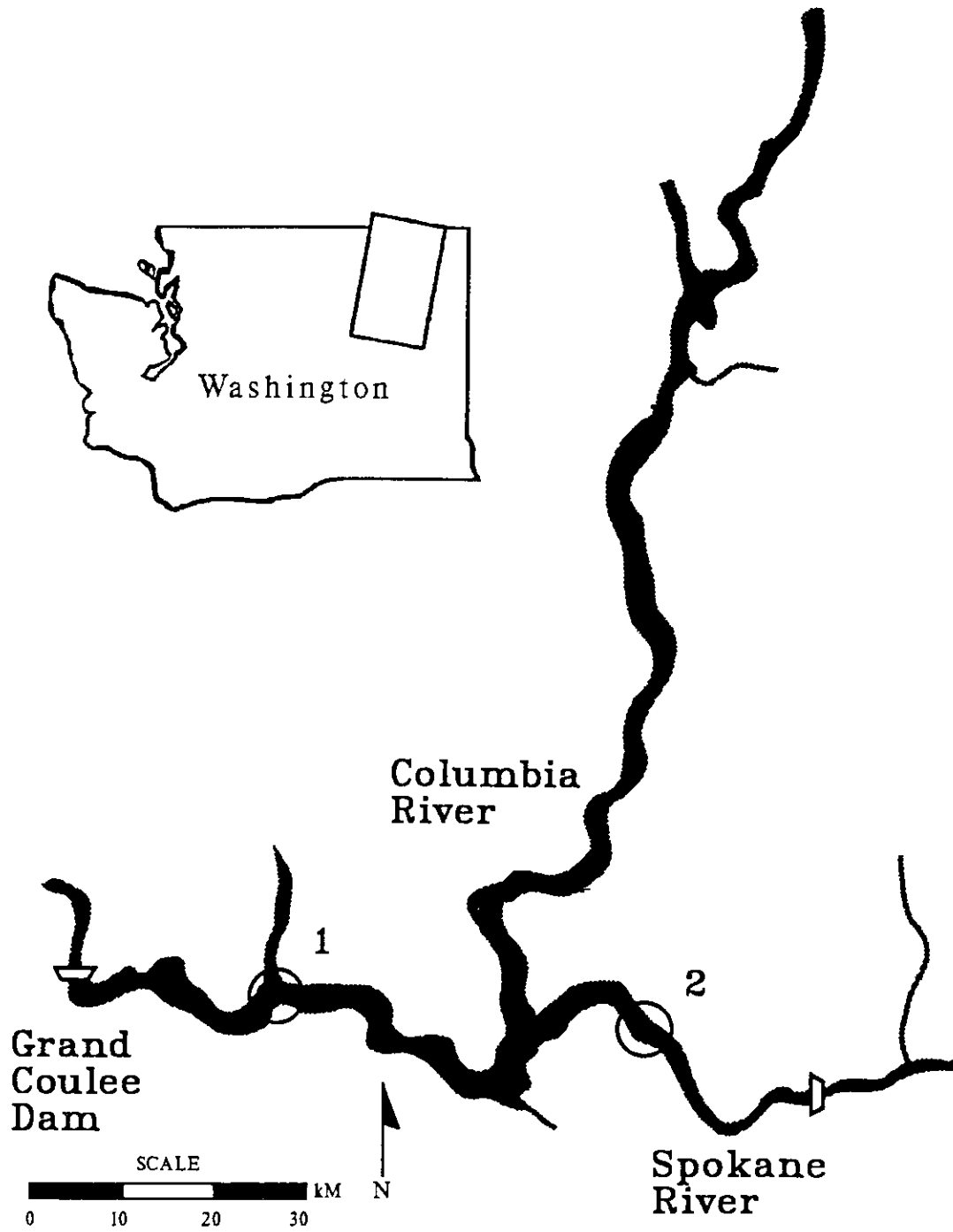


Figure 1. Location of sampling stations 1 (mouth of Sanpoil River) and 2 (Porcupine Bay), Lake Roosevelt, Washington.

regarding Lake Roosevelt prompted a fisheries and limnology investigation by the U.S. Fish and Wildlife Service (Beckman *et al.* 1985), of which the present study was a part.

Methods

Sampling was conducted at two stations in the lower reservoir: station 1, located at the mouth of the Sanpoil River, and station 2, within Porcupine Bay of the Spokane River arm (Figure 1). An embayment site and a tributary confluence site were sampled at each station.

We sampled larval fish and zooplankton weekly from 26 May to 7 July, 1982 during daylight hours. Larval fish were collected with 0.5-m plankton nets of 760-micrometer mesh. Zooplankton were collected with high-speed Miller samplers fitted with 153-micrometer nets. A 1.8-m outrigger extending from the inshore side of the bow of the boat was used to tow the nets just below the water surface, as close as possible to shore at each sampling site. The actual water depth of the sampled area was between 0.5 m and 2.0 m, and usually the nets sampled from the top, middle, and bottom of the water column simultaneously. In standard sampling procedure, a 10-minute tow for larval fish was followed by a 2-minute tow for zooplankton. Samples were washed into collection jars and preserved in 10% formalin.

Zooplankton samples were diluted or concentrated to a known volume and then subsampled with a large-bore pipette (3 to 5 subsamples). Zooplankters were enumerated from the subsamples by use of a plankton counting wheel on a dissecting microscope. We used mean number of organisms of a given taxon from the subsamples to estimate the density (number/m³) and percent composition by number for each station and date.

Zooplankters were classified to suborder (copepods), developmental stage (nauplii), or genus (Cladocera). Because morphological characteristics of larval largescale, bridgelip, and longnose (*Catostomus catostomus*) suckers were too similar to allow specific identification, they were combined in the analyses. For the same reason, prickly, mottled (*Cottus bairdi*), and torrent (*C. rhotheus*) sculpins were combined.

Stomach contents from a random subsample of at least 10 larvae of each taxon (walleye, yellow perch, sculpins, and suckers) were analyzed from each tow (if available). Total length of each fish was measured, and ingested organisms were iden-

tified to the lowest practical taxon and enumerated. Percent composition by number was determined for each prey taxon. Stomach contents data from embayment and confluence sites were pooled by date and station to provide sufficient sample sizes for analysis, assuming no differences between sites. Because fish size is not an independent variable of time, analyses of food preferences based on fish size were not performed. We assumed that analyses of preferences over time reflected changes in fish size.

A two-sided Wilcoxon's signed-rank analysis was used to test selectivity of larval fish for major prey taxa (Kohler and Ney 1982), with a null hypothesis of no difference in relative prey abundance between stomachs and zooplankton samples. Statistical significance was assumed at the $p < 0.05$ level.

We calculated diet overlaps among the four fish groups at each station, using the niche overlap index (d_{ij}) of Schoener (1970). Percentages used were the numerical percent composition of each major prey taxon (calanoid and cyclopoid copepods, copepod nauplii, *Bosmina* spp., *Daphnia* spp., *Leptodora kindtii*, *Ceriodaphnia* spp., and *Chydorus* spp.) in pooled stomachs of fish of a given taxon. Niche overlap values range from 0 (no overlap) to 1 (complete overlap); values above 0.60 are generally considered to indicate biologically important overlap (Zaret and Rand 1971, Wallace 1981), but not necessarily competition.

Results

Zooplankton

Dominant zooplankton taxa included daphnids, *Bosmina* spp., and cyclopoid (*Cyclops* spp.) and calanoid (*Diaptomus* spp.) copepods. Overall, mean zooplankton densities were much higher at station 1 (12,408/m³) than at station 2 (2,353/m³), with the exception of *Bosmina* spp., which was approximately 10 times as abundant at station 2 (52,900/m³ compared to 5,973/m³) toward the end of the sampling period.

Food Habits

Walleye: Major food items in the stomachs of the 80 larval walleye examined were calanoid and cyclopoid copepods (Table 1). Larval fish and the cladocerans *Leptodora kindtii*, *Daphnia* spp., and *Diaphanosoma* spp. contributed minor percentages to the walleye diet.

TABLE 1. Number of examined stomachs (n), range of total fish lengths (TL), and percent composition (by number) of major prey items in nonempty stomachs of larval fish in Lake Roosevelt, Washington, 1982.

	Walleye ¹	Yellow Perch ²	Sculpins	Suckers ³
STATION 1				
n	27	257	43	0
Range TL (mm)	8-24	5-25	6-11	
Calanoid	66	55	12	
Cyclopoid	21	23	73	
<i>Bosmina</i> spp.	0	0	0	
<i>Daphnia</i> spp.	3	12	15	
Other	9	11	0	
STATION 2				
n	53	92	65	143
Range TL (mm)	9-22	4-17	4-9	9-24
Calanoid	58	5	24	0
Cyclopoid	0	75	70	5
<i>Bosmina</i> spp.	2	11	0	49
<i>Daphnia</i> spp.	5	5	6	1
Other	35	4	0	45

¹Other prey taxa included primarily larval fish and *Leptodora kindtii*.

²Other prey taxa included primarily *Ceriodaphnia* spp. and *Leptodora kindtii*.

³Other prey taxa included primarily *Chydorus* spp.

Only walleye preyed on other larval fish. Stomachs containing larval fish seldom contained other food items. One of the smallest walleye (9mm) contained larval fish that were 3 to 6 mm long. Walleye, yellow perch, sculpins, and suckers were among the fish species eaten. The percentage of larval fish in walleye diets was up to seven times higher at station 2 than at station 1.

Temporal changes in percent composition of individual prey items in walleye stomachs were evident, as exploitation of calanoid and cyclopoid copepods generally followed fluctuations in abundance of those populations in the sampling areas (Figure 2). The low level of predation on cyclopoid copepods at station 2 was an exception in view of the high abundance of that prey in the water column.

Yellow Perch: Calanoid and cyclopoid copepods and *Daphnia* spp. were the principal food items in the 349 larval yellow perch stomachs examined; others included *Bosmina* spp., *Ceriodaphnia* spp., and *Leptodora kindtii* (Table 1). Calanoid cope-

pods were dominant prey in stomachs of yellow perch at station 1, and cyclopoid copepods were dominant at station 2.

Both abundance and consumption of *Daphnia* spp. peaked late in the sampling period. Percent composition of copepods in stomach samples also approximated seasonal changes in the density of copepods in the reservoir (Figure 2).

Sculpins: Of 108 larval sculpin stomachs examined, 40% were empty. Most of these were from station 2, where only half of the stomachs contained prey. Cyclopoid copepods were the most numerous prey, followed by calanoid copepods and *Daphnia* spp. (Table 1). Sculpin lengths were small (compared to other fish taxa analyzed), ranging from 4 to 11 mm.

Suckers: Of the 143 suckers examined (all from station 2), 85 contained prey in their stomachs. Most empty stomachs were from fish 10 to 12 mm long, which still had yolk sacs. *Bosmina* spp., *Chydorus* spp., and cyclopoid copepods were the most numerous food items (Table 1). Suckers were the only fish sampled that preyed extensively on *Bosmina* spp. or *Chydorus* spp. The use of cyclopoid copepods was highest early in the sample period and steadily declined towards the end (Figure 2). A temporal increase in the use of *Bosmina* spp. accompanied an increase in its availability in the water column (Figure 2). Percent composition of *Chydorus* spp. in sucker stomachs ranged from 2 to 9% in early June to 47 to 67% in late June, dropping to 23% during the final week of sampling. *Chydorus* spp. was rarely collected in zooplankton samples at anytime (Wunderlich 1985).

Selectivity and Diet Overlap

Selectivity values for eight prey items were averaged for each fish taxon across stations and dates (Table 2). Larval walleye exhibited positive selection only for calanoid copepods, while larval yellow perch exhibited selection for *Daphnia* spp., *Ceriodaphnia* spp., and calanoid and cyclopoid copepods. Sculpins preferred cyclopoid copepods, while suckers preferred *Bosmina* spp., *Chydorus* spp., and cyclopoid copepods. Yellow perch was the only species that preferred *Daphnia* spp., and only suckers preferred *Chydorus* spp.

The Schoener niche overlap value between walleye and yellow perch was significant ($d_{xy}=0.84$) at station 1. All other overlap values were below 0.35 except for those between yellow

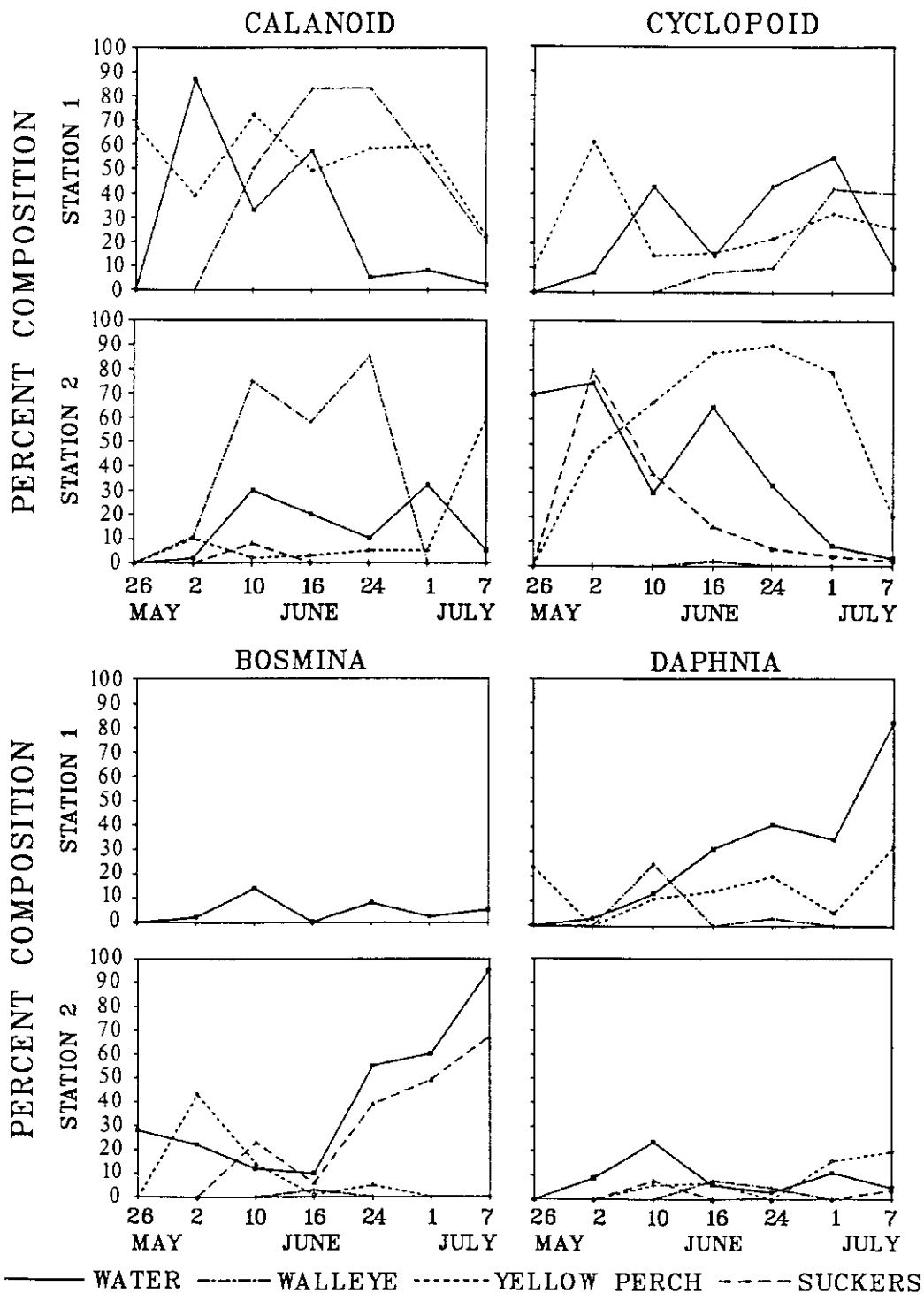


Figure 2. Percent composition (by number) of major prey items in the water column and in stomachs of larval walleye, yellow perch, and suckers in Lake Roosevelt, Washington, 1982.

TABLE 2. Larval fish selectivity values and probability values (p) from Wilcoxon's signed-rank comparison tests for eight prey items, Lake Roosevelt, Washington, 1982. + denotes positive selection, - denotes negative selection, and R denotes random selection.

Prey	Walleye (p)	Yellow perch (p)	Sculpins (p)	Suckers (p)
Copepods				
Calanoid	+(0.00)	+(0.00)	R(0.06)	R(0.05)
Cyclopoid	R(0.21)	+(0.00)	+(0.01)	+(0.00)
Nauplii	-(0.00)	-(0.00)	-(0.00)	-(0.00)
Cladocerans				
<i>Bosmina</i> spp.	-(0.00)	R(0.69)	-(0.00)	+(0.02)
<i>Daphnia</i> spp.	R(0.75)	+(0.00)	R(0.69)	R(0.24)
<i>Chydorus</i> spp.	-(0.00)	-(0.00)	-(0.00)	+(0.00)
<i>Ceriodaphnia</i> spp.	-(0.03)	+(0.01)	-(0.00)	R(0.11)
<i>Leptodora kindtii</i>	-(0.06)	-(0.00)	-(0.00)	-(0.00)

perch and sculpin, which were 0.50 at station 1 and 0.57 at station 2.

Discussion

The relatively greater densities of zooplankton at station 1 could have been a result of warmer water at the embayment site (temperature was measured in a concurrent study, as reported by Beckman *et al.* [1985]). Zooplankton abundance and epilimnetic temperature have been reported to be strongly correlated (Walburg 1972, Patalas and Salki 1984).

The significance of larval fish and *Leptodora kindtii* to larval walleye may have been underestimated due to the size differences between these food items (which were 3 to 10mm long) and other ingested zooplankters (which were 0.5-2.0mm long). This size difference suggests a greater contribution by fish and *Leptodora kindtii* to the walleye diet in terms of energy biomass than the numeric analyses indicate. Although walleye have generally been found to begin consuming larval fish at lengths between 30 and 62 mm (Forney 1966, Walker and Applegate 1976, Mathias and Li 1982), we found larval fish in the stomachs of walleye as small as 9mm. This discrepancy could have been due to patterns in prey availability, as similarly concluded by Mathias and Li (1982), and indicated by differences in prey availability between stations 1 and 2. Stomachs of walleye from sta-

tion 2 contained appreciably more larval fish than did those from station 1. Though abundance of larval fish (as prey) at station 2 was not markedly different from that at station 1 (Wunderlich 1985), calanoid copepods, the generally preferred prey of walleye overall, were much less abundant at station 2. Low densities of this preferred food item may have influenced walleye to begin feeding on larval fish at an earlier age than if calanoid copepods had been more abundant.

Larval walleye were selective for calanoid copepods, the largest zooplankters consistently encountered in Lake Roosevelt, even when other prey items were more abundant. The larger mouth gapes and better-developed teeth in larval walleye relative to larval yellow perch, sculpins, or suckers enable walleye to ingest larger prey (Mathias and Li 1982). Similar size selectivity has been documented for walleye elsewhere. Larval walleye in Oneida Lake, New York, were selective for cyclopoid copepods, which were larger than the co-occurring calanoid copepods in that system (Houde 1967). Walker and Applegate (1976) found positive selection for calanoid copepods, the largest prey available, in young-of-the-year walleye in South Dakota, while Mathias and Li (1982), in field and laboratory studies in Manitoba, observed a positive size selectivity for cyclopoid copepods.

Calanoid and cyclopoid copepods were major items in the diet of larval yellow perch in Lake Roosevelt. Yellow perch fed more heavily on copepods than on *Daphnia* spp., though selectivity values were positive for both. Yellow perch larvae depended on copepods in northern Minnesota (Siefert 1972), Iowa (Bulkley *et al.* 1976), and before they reached 30 to 35 mm in Oneida Lake, New York (Mills *et al.* 1984), but ate *Daphnia* spp. almost exclusively in Manitoba (Wong and Ward 1972) and in Oneida Lake after reaching 30 to 35 mm (Hansen and Wahl 1981, Mills *et al.* 1984). These dissimilarities may be explained by variation in geographical and temporal prey abundance. In the present study, utilization of *Daphnia* spp. was highest when they were at peak abundance in the water column.

Sculpins rapidly become benthic during early life stages (Sheldon 1968, Wallus and Granneman 1978), which would explain the patchy distribution (Wunderlich 1985) and small size of the sculpins we collected. Cyclopoid (76.4%) and calanoid copepods (8.3%) and *Daphnia* (15.3%) were the most important food items at station 1. The high

incidence of empty stomachs, similarly reported by Bailey (1952) for larval sculpins, indicated that exogenous feeding had not yet begun in many sculpins that were vulnerable to the collection gear. By the time complete exogenous feeding had begun, sculpins were probably able to avoid the townets or had become benthic.

Larval suckers ate *Bosmina* spp. and *Chydorus* spp., the smallest mature zooplankters sampled in Lake Roosevelt, almost exclusively. Mouth size of young-of-the-year suckers has been shown to limit food intake to small prey items (Stewart 1926, MacPhee 1960). Consumption of small cladocerans (as well as other prey) by larval suckers was reported from Idaho (MacPhee 1960) and from Shuswap Lake, British Columbia (Carl 1936). However, MacPhee (1960) did not find the degree of feeding specialization that we observed in Lake Roosevelt and labeled the feeding of larval suckers as "indiscriminate." Dependence of suckers on *Bosmina* spp., numerically the most abundant zooplankter at station 2, suggested that suckers in Lake Roosevelt were highly opportunistic, rather than indiscriminate feeders.

Because the bottom-dwelling *Chydorus* spp. was probably not effectively sampled by our towed nets, its use by fish was consistently greater than its apparent availability. Use of *Chydorus* spp. was expected to increase as suckers increased in size and adopted benthic feeding modes, as described by MacPhee (1960) and Stewart (1926), but no increase was seen in Lake Roosevelt. The influence of a highly abundant prey item (*Bosmina* spp.) appeared to have a greater effect on species selectivity than did the influence of changing feeding morphologies.

Overlap, defined as "the use, typically at the same time, by more than one organism of the same resource regardless of resource abundance," may indicate competition for a resource, which has been defined as "the demand, typically at the same time, of more than one organism for the same resource of the environment in excess of immediate supply" (Weatherly 1963, Zaret and Rand 1971). Diet overlap, then, could suggest competition for a shared prey resource only when that prey resource is in short supply (Hurlbert 1978, Abrams 1980).

Overlap values were high between walleye and yellow perch at station 1, with both species preying extensively on calanoid copepods. Though overall abundances of calanoid copepods were higher at station 1 than at station 2, there were seasonal periods of relatively low abundance. During those times, the use of calanoid copepods by both walleye and yellow perch was high (Figure 2). Overlap values and positive selection of calanoid copepods by both percids over a range of densities suggested that trophic competition between larvae of walleye and yellow perch in Lake Roosevelt was occurring. Our hypothesis that diets of larval percids in Lake Roosevelt would differ from those reported from other systems, due to unique co-occurring species, was rejected.

In a discussion of the controversy over interspecific competition, Schoener (1982) indicated that when competition occurs only seasonally during infrequent "lean" times, it is considered too weak to significantly influence character divergence or species exclusions. Because the indicated competition and the documented switch to alternate prey observed for walleye at station 2 was localized and of short duration, the potential effects of competition on growth, survival, and character divergence of walleye and yellow perch are considered minor in Lake Roosevelt. Since no between-year comparisons are available, the potential importance of competition is indicated only for the year studied. The importance of competition may be stronger or weaker than observed here, depending on conditions varying between years. In years when stronger competition occurs, it could have a larger effect on year-class strength, which is important to fishery managers.

Acknowledgements

We thank William Nelson, Anthony Nigro, and David Wahl for help with project design. The U.S. Fish and Wildlife Service, Seattle National Fishery Research Center, supplied funds through the U.S. Bureau of Reclamation. Technical review was provided by Dave Faurot, Ray Jones, Bill Nelson, as well as several anonymous reviewers. Ms. Dee Topp typed the final manuscript and Mark Koebbe assisted with the graphics.

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Received 16 March 1990

Accepted for publication 26 October 1993