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Ontogenetic Shifts in Habitat and Diet of Cutthroat Trout in Lake Washington, Washington

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Abstract.—Salmonids often display a series of ontogenetic shifts in habitat, and these may also be associated with changes in diet. For example, adfluvial populations rear in streams for several years and then migrate to lakes. The patterns of habitat use, trophic ecology, and movements of such populations are commonly studied during the riverine stages. The lacustrine period is typically less well known, but salmonids may play an important ecological role as lake piscivores. In Lake Washington, Seattle, Washington, cutthroat trout *Oncorhynchus clarki* are a top native piscivore and may affect the dynamics of the fish and zooplankton upon which they prey. Our objective was to study the growth, diet, and size distribution of cutthroat trout in littoral and limnetic habitats of Lake Washington, with emphasis on consumption of two of the lake's dominant pelagic planktivores: juvenile sockeye salmon *O. nerka* and longfin smelt *Spirinchus thaleichthys*. Cutthroat trout entered the lake at approximately age 2. As they grew larger, the cutthroat trout became increasingly piscivorous and tended to occupy the limnetic zone after they reached about 250 mm fork length (FL). Specifically, percentages (by wet weight) of fish in the diet of cutthroat trout increased from 22.5% for cutthroat trout smaller than 200 mm FL to over 95% for cutthroat trout larger than 400 mm FL. Fish made up a higher percentage of cutthroat trout diets in fall and winter in both the limnetic and littoral zones, and a greater proportion of fish was consumed in the limnetic zone than in the littoral zone. Variation in diet was observed among years (1995–2000), apparently reflecting the relative abundance of longfin smelt. The role of cutthroat trout both as the object of recreational fisheries and as a predator on sockeye salmon (valued in commercial and recreational fisheries) complicates management of this large, urban lake.

Salmonids are often the top piscivores in temperate and boreal lakes (Nilsson and Northcote 1981; Steward et al. 1981; Beauchamp et al. 1992), and their predation can affect fish assemblage structure. For example, Yule and Luecke (1993) suggested that piscivory by lake trout *Salvelinus namaycush* in Flaming Gorge Reservoir, Utah, altered the proportions and abundances of two important forage fish: Utah chub *Gila atraria* abundance decreased significantly, while kokanee *Oncorhynchus nerka* increased. Rowe (1984) described systemwide alterations in New Zealand's Rotorua lakes, and speculated that increased pre-

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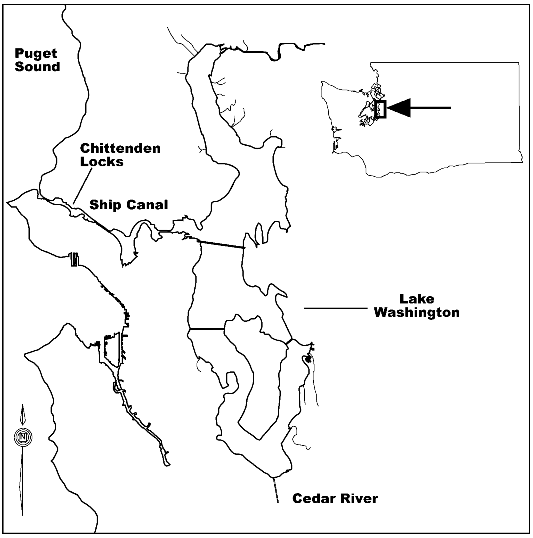

FIGURE 1.—Map of Lake Washington, Washington, showing the Cedar River (the lake's largest tributary). Solid lines across the lake indicate floating bridges.

dation by nonnative rainbow trout *O. mykiss* on the native common smelt *Retropinna retropinna* could contribute to eutrophication of smaller lakes. In many lakes in western North America, cutthroat trout *O. clarki* are an important piscivore (Hazzard and Madsen 1933; Neilson and Lentsch 1988; Reimchen 1990) and an important predator of juvenile salmonids (Beauchamp et al. 1995; Cartwright et al. 1998; Baldwin et al. 2000). Therefore, cutthroat trout may affect the population dynamics of salmonids and other fish species.

Trophic effects are not necessarily confined to specific prey species but may change with increasing predator size. Ontogenetic shifts in size are reflected in changes in habitat, diet composition, and foraging tactics (Keeley and Grant 2001). Larger fish are able to capture and consume larger prey items, and their lower risk of predation enables larger fish to forage with fewer constraints than smaller fish (Hughes 1997). Juvenile cutthroat trout may shift their feeding behavior and diet composition as they grow. Luecke (1986) found that cutthroat trout smaller than 60 mm tended to eat plankton, but those at least 70 mm in length consumed larger, benthic prey items. Large cutthroat trout are often piscivorous, but they can feed on a broad range of prey species, including zooplankton and benthic invertebrates (Andrusak and Northcote 1971; Chess et al. 1993).

Lake Washington (Figure 1) is one of the more closely studied lakes in western North America. This monomictic lake in western Washington near Seattle has gone through many changes over the past 100 years (Edmondson 1991). The excavation of the Lake Washington Ship Canal and the installation of the Hiram Chittenden Locks between the lake and Puget Sound (forming a new outlet for the lake) lowered the lake's level by about 3 m (Ajwani 1956). The Cedar River was also diverted into Lake Washington (presently contributing about half of the lake's water), further altering the hydrology of the lake. Numerous nonnative fish species have been introduced into the lake, mostly in the early part of the 20th century (E. Warner, unpublished data). During the mid-20th century, a large, escalating eutrophication event was remedied by diverting sewage from the lake (Edmondson 1991).

The early history of cutthroat trout in Lake Washington is unknown. As recently as the 1960s and 1970s, this species was not abundant enough to be considered a significant ecosystem component in a comprehensive trophic study of the Lake Washington ecosystem (Eggers et al. 1978). At that time, the northern pikeminnow *Ptychocheilus oregonensis* was considered the dominant piscivore. By the 1990s, anecdotal evidence indicated the existence of a large, adfluvial population of cutthroat trout that could affect the ecology of the lake by inducing cascading effects on planktivores and plankton. Cutthroat trout in Lake Washington were reported to feed primarily on two planktivores: longfin smelt *Spirinchus thaleichthys* and juvenile sockeye salmon *O. nerka* (Beauchamp et al. 1992). Longfin smelt were apparently absent or rare in the lake until the late 1950s, and sockeye salmon were scarce until the 1960s (Edmondson 1991), but both species are presently numerous. The longfin smelt mature primarily at age 2 in Lake Washington, and the odd- and even-year cohorts differ dramatically in abundance. Longfin smelt spawn primarily from February through mid-April in the lower 2 km of the Cedar River (Moulton 1974), and they die shortly after spawning. Typically, even-year spawning classes are 5–15 times more abundant than odd-year classes (Beauchamp 1987). From May to December, age-0 longfin smelt abundance is much lower in odd-numbered years than in even years, and age-1 fish abundance is much lower in even-numbered years than in odd years (Chigbu 1993). This dramatic annual variation in longfin smelt abundance might affect the level of predation on juvenile sockeye salmon that enter the lake as fry in winter and spring, and leave for the ocean 1 year later.

The overall purpose of this study was to determine the ontogenetic changes in habitat (littoral and limnetic) and trophic ecology of cutthroat trout in Lake Washington, with special emphasis on sockeye salmon as prey. The specific objectives were as follows: (1) to determine the ages and sizes at which cutthroat trout enter the lake from streams and shift from littoral to limnetic habitats, and (2) to describe the effects of body size, season, year, and habitat on cutthroat trout diet. We hypothesized that the percentage of fish in the diet would increase with cutthroat trout size, and would vary in response to changes in the relative abundances of sockeye salmon and longfin smelt. Seasonal shifts in diet were expected based on the sizes of juvenile sockeye salmon and longfin smelt. Larger sockeye salmon emigrate from the lake as smolts in the early summer, and age-0 sockeye salmon enter the lake from streams in early spring. We also predicted that greater piscivory would occur in the limnetic zone, where sockeye salmon and longfin smelt are abundant, than the littoral zone (Eggers 1978; Chigbu 1993).

Methods

From February 1995 through January 2000, a total of 1,151 cutthroat trout was collected in Lake Washington's littoral and limnetic zones. The littoral zone was defined as the region of the lake with bottom depths less than 15 m, and the limnetic zone was defined as the region with depths of 15 m or greater, following Beauchamp (1990). The littoral zone, thus defined, accounts for 18.6% of the lake's area (C. P. Gubala, JC Headwaters, Inc., and JC Headwaters Canada, Ltd., unpublished data). Sampling was conducted by the U.S. Fish and Wildlife Service (USFWS), Washington Department of Fish and Wildlife (WDFW), Muckleshoot Indian Tribe (MIT), and the University of Washington (UW). Samples originated from a lakewide study of juvenile sockeye salmon ecology. Effort was not allocated evenly among years or between areas of the lake. We therefore pooled the samples across years and areas. By pooling our data across multiple years, we believed our comparisons would be less sensitive to the effects of any one year. In the littoral zone, cutthroat trout were collected by 257 beach-seine sets and 110 gill-net sets, and by electrofishing along a total shoreline length of 71.5 km. Gillnetting was conducted throughout the lake; beach seining and electrofishing were done in the southern and northern parts of the lake. Cutthroat trout in the limnetic zone were primarily collected by purse seining (108 sets) and gillnetting (136 sets) throughout the lake. Bottom trawls (106 sets) were also conducted in the limnetic zone, but few cutthroat trout were captured. Regardless of capture method, cutthroat trout were anesthetized, measured for fork length (FL), and weighed. Scales were removed from a subsample of fish and were pressed onto acetate cards, and the annuli were counted under a dissection microscope for age determination.

Stomach samples were collected with gastric lavage from 817 cutthroat trout (an additional 158 fish had empty stomachs). The gut contents were stored on ice in the field, and then frozen for later analysis. In the laboratory, the total wet weight of the stomach contents was recorded, as were the numbers and wet weights of prey items identified to the lowest possible taxonomic level. Stomach content samples were sorted into seasons, cutthroat trout size-classes, and prey categories. Seasons were designated as winter (January–March), spring (April–June), summer (July–September), and fall (October–December). Four size-classes of cutthroat trout (100–199 mm, 200–299 mm, 300–399 mm, and >400 mm FL) were chosen based on size-frequency data. We chose eight prey categories (sockeye salmon, salmonids, longfin smelt, other fish, mysid shrimp *Neomysis* spp., zooplankton, other invertebrates, and other) based on the resolution of the taxonomic classification and our particular interest in piscivory. The salmonid category included unidentified salmonids; this category may have included many sockeye salmon that were too digested for full identification. To reduce the number of unidentified salmonids, genetic analysis was performed on some samples by use of either DNA sequencing or mitochondrial DNA analysis. Methodologies were similar to those used by Purcell et al. (2004) except that muscle tissue was analyzed instead of bones. To normalize prey weight based on predator weight, and to express the importance of the prey categories relative to predator size (Hyslop 1980), prey category data were reported as mean weight (g) consumed, mean percentage of the predator's body weight, or mean percentage of the diet for cutthroat trout from a given size-class, season, or habitat. The weight of prey consumed and the relative prey weights were calculated for individual cutthroat trout. These data were then summed for all cutthroat trout sampled, and the mean was calculated based on the sample size for the given size-class, season, or habitat.

The size-frequency distribution of cutthroat trout collected in Lake Washington was calculated for both the littoral and limnetic habitats. These areas were not sampled with equal intensity; the effort in the littoral zone was about 5–10 times greater than that of the limnetic zone on a rough, per-area basis. However, given the differences in efficiency among gear types and the varied effort among years, we elected to use simple size-frequency distributions to show the percentages of fish sampled within each habitat, rather than attempting to estimate the overall size-frequency distribution in the entire lake.

Additional analysis was conducted to relate the individual sizes of the most common fish prey (sockeye salmon, unidentified salmonids, longfin smelt, sculpins *Cottus* spp., and threespine sticklebacks *Gasterosteus aculeatus*) to the sizes of their cutthroat trout predators. Prey lengths were either obtained directly from the sample or from regressions that extrapolated certain morphometrics into FL for partially digested fish. Most of the conversion regressions were from the published literature (Hansel et al. 1988; Vigg et al. 1991), but we developed several regressions for longfin smelt by following the procedures of Hansel et al. (1988) (FL = 1.725 + 1.082[standard length]; FL = 4.916 + 1.287[nape-to-tail length]; FL = 9.802 + 8.424[cliethrum length]; FL = −7.359 + 13.065[dentary length]; N = 35; range = 67–117 mm FL; $r^2 \geq 0.94$). Due to the importance of certain prey fish in the diet of cutthroat trout (determined by frequency of occurrence), and the level of digestion of certain prey fish, not all fish found in the collected stomach contents were used in this analysis (measurements from 482 of 2,100 fish were used). Size data for fish prey were presented relative to predator size data for all cutthroat trout, and then were separated by habitat. To determine which year-classes of longfin smelt were consumed by cutthroat trout, we estimated the age of ingested longfin smelt based on age and growth data from Moulton (1974).

Results

Size Composition and Growth

Cutthroat trout apparently recruited to Lake Washington from streams at about 150 mm FL, as few fish (11.0%) below this size were captured in the lake (all fish > 150 mm were captured in the littoral zone). Analysis of scale samples indicated that cutthroat trout were primarily age 2 when they entered the lake, and that their subsequent growth was rapid (Table 1). However, because no fish smaller than 150 mm were analyzed, we cannot dismiss the possibility that some fish may recruit to the lake at age 1. The cutthroat trout in the littoral zone (mean FL = 201.8 mm; N = 722) were much smaller than those in the limnetic zone (mean FL = 372.8 mm; N = 425; t = 30.71; $P <$ 0.001; Figure 2). The smallest sizes of collected cutthroat trout were 90 mm FL in the littoral zone and 150 mm FL in the limnetic zone.

TABLE 1.—Mean fork length (FL) and weight at age for cutthroat trout in Lake Washington, Washington, 1995–2000. Lengths were directly measured, but in some cases, weight was estimated from length (weight = (5×10^{-6}) $FL^{3.149}$ (r^2 = 0.98).

Age	N	Fork length (mm, SD)	Weight (g, SD)
2	8	193.3 (25.1)	72.9 (40.1)
3	19	296.6 (90.6)	401.2 (614.4)
4	21	362.8 (73.1)	641.5 (438.7)
5	12	471.8 (35.8)	1,240.3 (258.4)
6	3	490.7 (32.3)	1,525.8 (538.8)
7	1	519.0	1,774.3

Effects of Size, Season, and Habitat on Diet

Cutthroat trout ate various fishes and invertebrates, but consumed a greater percentage of fish as they increased in size (Tables 2, 3). The combined percentage of fish (sockeye salmon, salmonids, longfin smelt, and other fish) in the diet of littoral cutthroat trout increased from 18.8% for 100–199-mm trout to 41.7% for 200–299-mm trout, 78% for 300–399-mm trout, and 97.8% for the largest size-class (>400 mm). Similarly, in the limnetic zone, the combined percentage of fish in the diet increased from 61.4% for 200–299-mm trout to 94.3% for 300–399-mm trout and 99.6% for cutthroat trout larger than 400 mm. Fish made up 96.6% of the diet of small cutthroat trout (100–199 mm) in the limnetic zone, but the results may not have been representative, due to the small sample size (N = 7). Cutthroat trout of the 100–199-mm size-class ate mostly invertebrates (63.7%) other than zooplankton and *Neomysis* spp. The ''other invertebrates'' category consisted primarily of oligochaetes, chironomids, trichopterans, ephemeropterans, megalopterans (*Sialis* spp.), and terrestrial insects. The zooplankton consumed by cutthroat trout consisted almost entirely of cladocerans *Daphnia* spp.

As hypothesized, fish (sockeye salmon, salmonids, longfin smelt, and other fish combined) constituted a greater proportion of the diet in the limnetic zone than in the littoral zone for each cutthroat trout size-class during most seasons (Tables

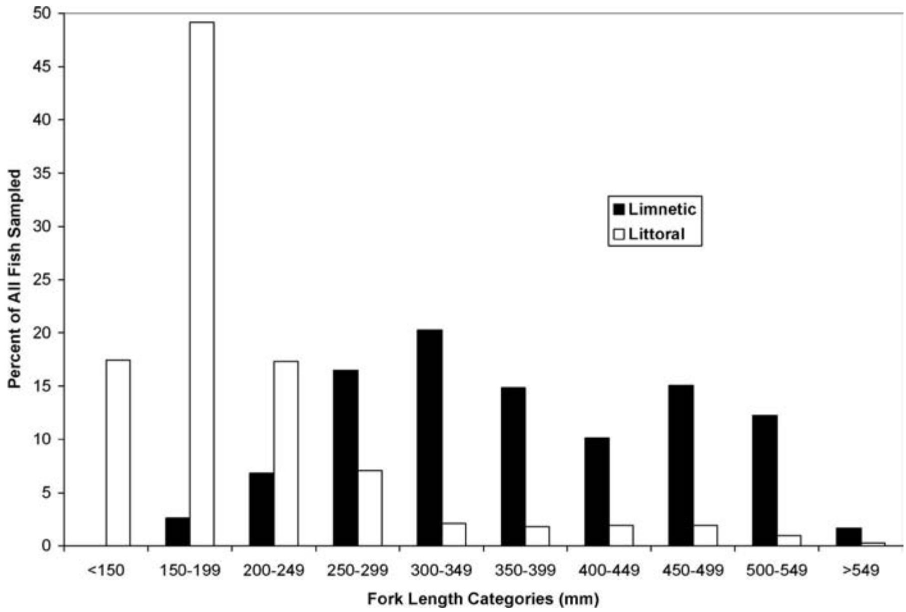

FIGURE 2.—Size-frequency distributions of cutthroat trout sampled in limnetic habitats (N = 425 fish) and littoral habitats (N = 722 fish) of Lake Washington, 1995–2000.

2, 3). The diet of cutthroat trout in the limnetic zone was generally less diverse than the diet in the littoral zone. In the limnetic zone, the diet was composed primarily of longfin smelt, sockeye salmon, zooplankton, and threespine sticklebacks. When combined, these four prey types made up 93% of the overall diet. For most seasons and cutthroat trout size-classes, zooplankton made up a

TABLE 2.—Diet (%) of four size-classes (FL, fork length) of cutthroat trout in the littoral zone of Lake Washington, 1995–2000. The sample size (N) only includes fish that had prey items in their stomachs. Other salmonids included mostly unidentified salmonids and some juvenile Chinook salmon.

Size-class (mm FL) and season	*N*	Sockeye salmon	Other salmonids	Longfin smelt	Other fish	*Neomysis*	Zooplankton	Other invertebrates	Other
100–199									
Winter	82	13.3	9.92	0.00	9.41	0.14	0.12	64.12	2.94
Spring	278	1.89	0.50	0.95	9.03	0.49	7.55	68.60	10.98
Summer									
Fall	1	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
200–299									
Winter	56	6.82	0.91	46.96	3.36	0.40	0.02	38.24	3.30
Spring	72	0.17	0.23	18.91	12.37	0.41	1.57	59.36	6.99
Summer	2	0.00	0.00	0.00	4.85	0.00	0.00	0.00	95.15
Fall	1	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00
300–399									
Winter	8	58.00	0.00	25.82	2.25	0.00	0.00	12.63	1.30
Spring	6	47.59	0.00	8.53	0.00	0.07	37.65	6.17	0.00
Summer	1	0.00	0.00	0.00	0.00	0.00	75.00	25.00	0.00
Fall	5	9.08	18.04	56.31	4.35	0.17	7.38	4.68	0.00
>400									
Winter	6	0.00	0.00	56.47	33.58	0.00	0.00	8.45	1.50
Spring	9	2.83	0.00	56.83	39.56	0.00	0.00	0.76	0.01
Summer	1	0.00	0.00	0.00	100.00	0.00	0.00	0.00	0.00
Fall	4	0.00	0.00	82.69	5.98	0.00	10.72	0.60	0.00

TABLE 3.—Diet (%) of four size-classes of cutthroat trout in the limnetic zone of Lake Washington, 1995–2000. The sample size (*N*) only includes fish that had prey items in their stomachs. Other salmonids included only unidentified salmonids.

Size-class (mm FL) and season	*N*	Sockeye salmon	Other salmonids	Longfin smelt	Other fish	*Neomysis*	Zooplankton	Other invertebrates	Other
100–199									
Winter	2	0.00	0.00	98.62	1.25	0.00	0.00	0.13	0.00
Spring	2	0.00	0.00	0.00	0.93	0.00	51.90	47.18	0.00
Summer	2	0.00	0.00	0.00	29.66	0.00	0.00	34.29	36.05
Fall	1	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00
200–299									
Winter	26	50.75	0.04	34.67	8.70	0.11	0.01	5.68	0.04
Spring	25	32.92	2.95	9.30	0.28	0.00	36.47	17.70	0.39
Summer									
Fall	18	7.93	2.25	14.04	11.75	0.17	38.82	24.06	0.98
300–399									
Winter	47	41.06	0.12	51.29	5.15	0.05	0.03	1.16	1.14
Spring	33	46.14	0.09	44.14	0.44	0.19	6.93	1.77	0.31
Summer									
Fall	27	0.00	0.42	81.28	7.79	0.12	8.74	0.04	1.62
>400									
Winter	42	59.35	0.04	25.19	14.85	0.00	0.00	0.28	0.30
Spring	20	90.74	0.02	3.11	5.19	0.64	0.21	0.08	0.01
Summer									
Fall	40	11.14	0.30	84.76	3.55	0.00	0.00	0.00	0.24

higher percentage of the diet in the limnetic zone than in the littoral zone (Tables 2, 3). In the littoral zone, cutthroat trout apparently fed throughout the water column, including in their diet various types of benthic prey, such as oligochaetes, fish eggs, sculpins, crayfish, leeches, amphipods, isopods, and mollusks. In contrast, cutthroat trout in the limnetic zone rarely ate benthic prey. Additionally, aquatic and terrestrial insects were common in the diet of cutthroat trout from the littoral zone but uncommon in the diet of fish from the limnetic zone.

Consumption of sockeye salmon was most pronounced in the winter and spring (Tables 2, 3). Sockeye salmon made up a small part of the diet of cutthroat trout during the fall. Sockeye salmon fry (24–40 mm FL) were observed primarily in the stomachs of 100–299-mm cutthroat trout from the littoral zone. Sockeye salmon fry were rare in the diets of larger fish (>300 mm) from the littoral zone and all fish from the limnetic zone. Larger juvenile sockeye salmon (60–140 mm) were an important component of the diet of cutthroat trout larger than 200 mm that were sampled in the limnetic zone. Larger juvenile sockeye salmon comprised 50% of the winter diet and 57% of the spring diet, averaged over the four size-classes of cutthroat trout.

We estimated ages for 206 of the 241 longfin smelt observed in stomach samples. When even-year spawning classes of longfin smelt were abundant as age-1 fish (May–December during odd years, January–April during even years), 96% of the longfin smelt consumed (N = 106) were age-1 fish. Likewise, when even-year spawning classes of longfin smelt were abundant as age-0 fish, 61% of the longfin smelt consumed (N = 100) were age-0 fish. Consistent with the hypothesis that longfin smelt might absorb some of the predation pressure from salmonids, lower percentages of sockeye salmon were eaten by cutthroat trout when even-year spawning classes of longfin smelt were abundant as age-1 fish (Table 4). In the limnetic zone, longfin smelt made up 68% and sockeye salmon made up 12% of the overall cutthroat trout diet when even-year spawning classes of longfin smelt were abundant as age-1 fish. In contrast, longfin smelt made up 34% of the diet and sockeye salmon comprised 50% of the diet when even-year spawning classes of longfin smelt were abundant as age-0 fish. A similar trend, although not as dramatic, was observed in the littoral zone (Table 4).

Analysis revealed positive relations between the size of cutthroat trout and the size of prey fish eaten in both limnetic and littoral habitats (Figures 3, 4). Within the limnetic zone, cutthroat trout length was positively related to the size of all prey fish combined (N = 227; r^2 = 0.18; analysis of

TABLE 4.—Diet (%) of cutthroat trout in the littoral and limnetic zones of Lake Washington, 1995–2000, when even- or odd-year spawning classes of longfin smelt were present as age-1 fish. The even-year spawning classes of longfin smelt were abundant as age-1 fish in May–December during odd years and January–April during even years. The odd-year spawning classes were abundant as age-1 fish in May–December during even years and January–April during odd years. Adult longfin smelt spawning occurs from February to April. Samples from different seasons and years were pooled together. The sample size (N) only includes cutthroat trout that had prey items in their stomachs. Other salmonids included mostly unidentified salmonids and some juvenile Chinook salmon.

Habitat and longfin smelt year-class	Cutthroat trout (N)	Sockeye salmon	Other salmonids	Longfin smelt	Other fish	*Neomysis*	Zooplankton	Other invertebrates	Other
Littoral									
Even	280	2.74	1.69	11.60	8.68	0.34	0.56	65.46	8.92
Odd	252	9.34	4.40	5.06	10.16	0.40	9.59	55.24	5.82
Limnetic									
Even	122	12.03	0.25	67.87	5.69	0.04	8.74	5.19	0.09
Odd	163	49.89	0.69	34.23	6.05	0.14	4.71	2.89	1.39

variance [ANOVA], $F = 30.3$, $P < 0.001$). Cutthroat trout length was also related to the sizes of sockeye salmon ($N = 98$; $r^2 = 0.19$; ANOVA, $F = 22.7$, $P < 0.001$) and longfin smelt ($N = 97$; $r^2 = 0.11$; ANOVA, $F = 11.4$, $P = 0.001$), but not to threespine stickleback size ($N = 15$; $r^2 = 0.06$; ANOVA, $F = 0.85$, $P = 0.37$). The length of cutthroat trout in the littoral zone was positively related to the size of all prey fish combined ($N = 255$; $r^2 = 0.46$; ANOVA, $F = 213.2$, $P < 0.001$), as well as to the sizes of sockeye salmon ($N = 133$; $r^2 = 0.46$; ANOVA, $F = 100.7$, $P < 0.001$), longfin smelt ($N = 54$; $r^2 = 0.14$; ANOVA, $F = 8.6$, $P = 0.005$), and sculpins ($N = 29$; $r^2 = 0.31$; ANOVA, $F = 12.2$, $P = 0.002$). The mean length of prey fish (not including larval fish) consumed by 100–199-mm cutthroat trout was 32 mm FL (maximum = 78 mm FL), compared to 54 mm FL (maximum = 112 mm FL) for 200–299-mm trout, 78 mm FL (maximum = 148 mm FL) for 300–399-mm trout, and 94 mm FL (maximum = 140 mm FL) for cutthroat trout larger than 400 mm. For each size-class of cutthroat trout, prey fish consumed in the limnetic zone was typically larger than those consumed in the littoral zone (Figures 3, 4). In addition to the prey fish displayed in Fig-

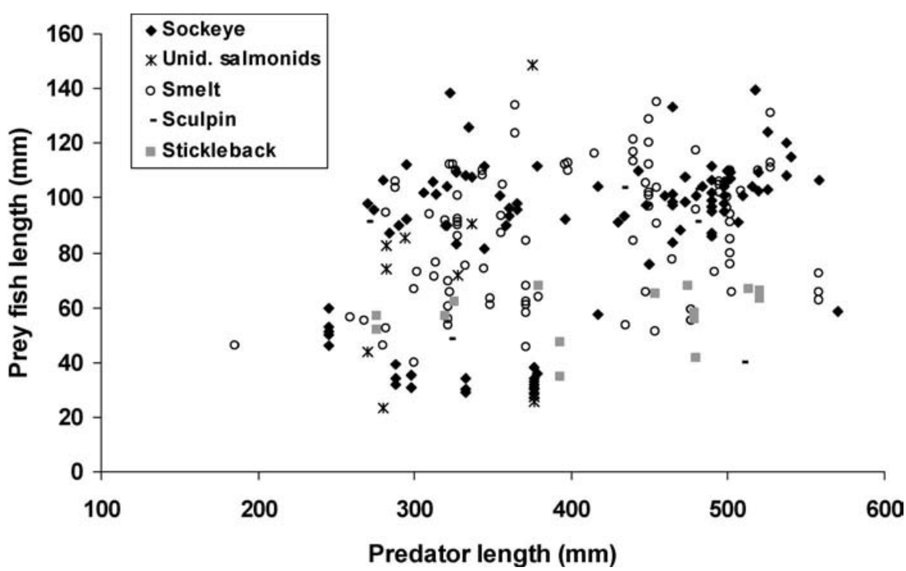

FIGURE 3.—Relations between predator fork length and the lengths of prey fish consumed by cutthroat trout in the limnetic zone of Lake Washington, 1995–2000. Prey groups are sockeye salmon, unidentified salmonids, longfin smelt, sculpins, and threespine sticklebacks.

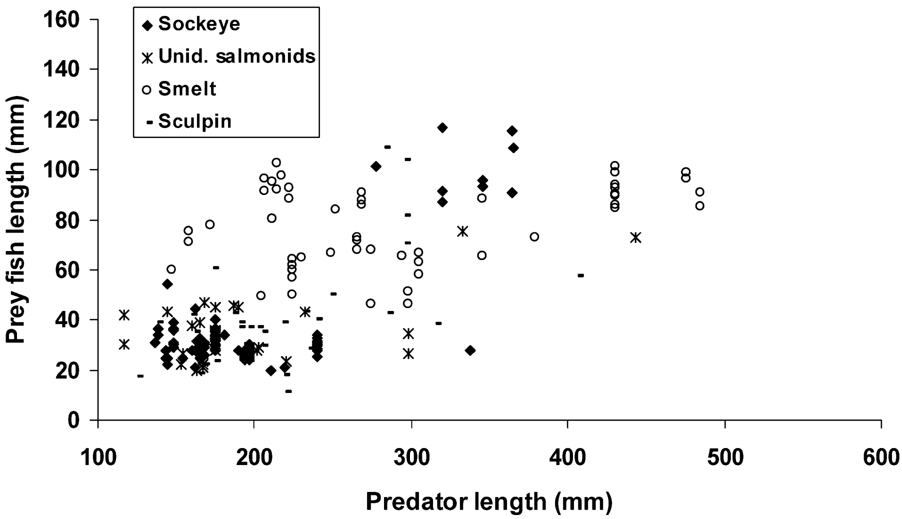

FIGURE 4.—Relations between predator fork length and the lengths of prey fish consumed by cutthroat trout in the littoral zone of Lake Washington, 1995–2000. Prey groups are sockeye salmon, unidentified salmonids, longfin smelt, and sculpins.

ures 3 and 4, large numbers of larval catostomids (*N* = 1,120; range = 13–16 mm total length [TL]) and other larval fish (*N* = 231; range = 8–17 mm TL) were also consumed by cutthroat trout, primarily in late spring. Consumption of larval fish was the most pronounced in 100–199-mm cutthroat trout sampled in the littoral zone (81% of all larval fish ingested).

Overall, we were able to identify 81% of the ingested salmonids to species. All of the identifiable salmonids in the limnetic zone were sockeye salmon (*N* = 132), as were 95% of the identifiable salmonids in the littoral zone (*N* = 153). Therefore, we assumed that the vast majority of unidentified salmonids were also sockeye salmon. Seventy-five percent of the unidentified salmonids were fry. Based on capture date and fish size, they were most likely sockeye salmon fry, which were present in large numbers in Lake Washington. The only other salmonid species observed in the stomach samples was juvenile Chinook salmon *O. tshawytscha* (*N* = 8).

Discussion

Size, Growth, and Diet

Although there was a wide variation in size at age, we found that cutthroat trout typically recruited into Lake Washington when they were 2 years old. Cutthroat trout spawn in several streams draining directly into Lake Washington or nearby Lake Sammamish, and electrofishing surveys in these tributaries routinely catch many cutthroat trout in their first and second years of life, but rarely catch larger, older cutthroat trout (K. L. Fresh and T. P. Quinn, unpublished data). Similarly, in coastal British Columbia lakes with sympatric populations of rainbow trout and cutthroat trout, the smallest lacustrine cutthroat trout ranged from approximately 125 to 225 mm (reviewed by Nilsson and Northcote [1981]).

Our results suggest that small (age 2) cutthroat trout enter the lake from streams and predominately occupy the littoral zone while temperatures are below stressful levels (late fall, winter, and early spring). During this time, the cutthroat trout eat insects and some fish. Littoral zone temperatures can exceed 17°C by mid-June (K. L. Fresh, unpublished data), and dissolved oxygen levels can become critically low near macrophyte beds (Frodge et al. 1995). As a result, cutthroat trout vacate shallower parts of the littoral zone in summer. It is unclear where they move to at this time. Since small cutthroat are rarely observed in offshore areas, we speculate that they may either move to cooler water within deep areas of the littoral zone (where we did not sample) or enter tributaries for several months. These smaller cutthroat trout then reoccupy the littoral zone as water temperatures cool in the fall.

As the cutthroat trout grow larger, they shift to the limnetic zone. Because large individuals are rarely found in the littoral region except in spring (Nowak and Quinn 2002), we interpret this habitat shift to be ontogenetic rather than a response to stressful environmental conditions. The large cutthroat trout prey more heavily on fish than do smaller cutthroat trout, and the prey fish that they consume are of a larger size in the limnetic zone versus the littoral zone. Large fish have a larger gape (Hughes 1997), and the size at which the cutthroat trout shifted their diet to fish is consistent with the data from a variety of salmonids, as reviewed by Keeley and Grant (2001). The tendency for piscivores to consume larger prey as they increase in size is commonly observed in many species (Mittelbach and Persson 1998). Therefore, cutthroat trout focus on large prey such as fish to maximize the amount of calories eaten per item. Luecke (1986) found that, although larger cutthroat trout were able to eat a wide range of prey, they ate fewer small items such as *Daphnia* spp. as they grew larger. Beauchamp et al. (1992) also reported that Lake Washington cutthroat trout shifted from smaller invertebrate prey to fish (sockeye salmon, longfin smelt, threespine sticklebacks, and prickly sculpin *Cottus asper*) as they grew. Similarly, the diet of 400–600-mm lake trout in Flaming Gorge Reservoir was more varied (including invertebrates and fish) than the diet of lake trout larger than 600 mm, which was comprised almost entirely of fish (Yule and Luecke 1993).

For cutthroat trout in Lake Washington, the ontogenetic habitat shift from the littoral zone to the limnetic zone appears to occur at approximately 200–300 mm FL. Similar habitat shifts have been observed for other lacustrine salmonids, such as rainbow trout (Tabor and Wurtsbaugh 1991; Landry et al. 1999) and Arctic char *Salvelinus alpinus* (L'Abee-Lund et al. 1993). The size at which fish move to the limnetic zone may reflect an interrelationship between predation risk and prey availability (Werner and Hall 1988). Preferred prey, such as forage fish and zooplankton, are often more available in the limnetic zone, but salmonids will not inhabit this zone until they are no longer vulnerable to most pelagic predators. Landry et al. (1999) found that age-0 rainbow trout in a small lake devoid of large trout were found primarily in the limnetic zone, where zooplankton levels were higher than in other areas. In a lake containing large trout, age-0 rainbow trout were mostly found in littoral and benthic habitats, and habitat choice was not based on zooplankton abundance. When Arctic char fry were stocked into a fishless lake in Norway, they began to inhabit the pelagic zone at 70–90 mm, whereas fry stocked into a lake containing predatory brown trout *Salmo trutta* waited until they were 150 mm to inhabit pelagic areas (Langeland and L'Abee-Lund 1998). L'Abee-Lund et al. (1993) found that the size of the smallest Arctic char in the pelagic zone of five Norwegian lakes was positively related to the size of the largest brown trout predators. In Lake Washington, both large cutthroat trout and large northern pikeminnow (i.e., >500 mm FL) are potential predators of juvenile cutthroat trout. Northern pikeminnow are rarely found in littoral areas until water temperatures warm, which occurs at the same time that small cutthroat seasonally vacate the littoral zone. As we have reported here, large cutthroat trout are rare in littoral areas. Additionally, the use of the limnetic zone by small cutthroat trout may also be influenced by avian predators, such as double-crested cormorants *Phalacrocorax auritus*, which preyed heavily on subadult trout in a southern Utah reservoir (Modde et al. 1996).

Although large numbers of sockeye salmon fry enter Lake Washington in the winter and spring, they are rarely consumed by the large cutthroat trout that inhabit the limnetic zone. In some years, as many as 38 million sockeye salmon fry enter Lake Washington (D. Seiler, WDFW, unpublished data). Upon entering the lake, sockeye salmon fry typically spend a few days or weeks in the littoral zone, but afterwards they are primarily found in the limnetic zone. Sockeye salmon fry made up less than 1% of the winter and spring diets of cutthroat trout in the limnetic zone. For winter and spring combined, we sampled 197 cutthroat trout in the limnetic zone, yet only eight had consumed sockeye salmon fry. Additionally, we found no evidence of fry predation in cutthroat trout larger than 400 mm. Instead of fry, limnetic cutthroat trout consumed large prey fish, such as longfin smelt (age 1), sockeye salmon presmolts, and threespine sticklebacks.

Based on our results, sockeye salmon fry that move to the limnetic zone may reduce their risk of predation and thereby avoid littoral predators, such as small cutthroat trout, juvenile coho salmon *O. kisutch*, rainbow trout, and prickly sculpin. A similar strategy has been suggested for other fish, including larval yellow perch *Perca flavescens* (Whiteside et al. 1985) and larval bluegill *Lepomis macrochirus* (Werner and Hall 1988). An additional explanation for the shift of sockeye salmon fry to limnetic habitats is that their primary food items are most abundant in limnetic areas (Burgner 1991).

The diets of cutthroat trout in littoral and limnetic habitats may reflect seasonal changes in prey availability and temperature. Diet comparisons between habitat types are complicated by the relation between diet and size, as large cutthroat trout dominated the limnetic zone. Because larger cutthroat trout are mostly limnetic (Nowak and Quinn 2002), their ability to feed on fish in open water during the summer may be restricted to the cooler water depths below the thermocline (Beauchamp 1994). However, large cutthroat trout may actually benefit from this position, because the prey fish (sockeye salmon and longfin smelt) must travel past them twice each day: once during their dusk migration to surface waters to feed on plankton, and again on the return to deep water during the day.

We collected few cutthroat trout stomach samples in summer (July–September), making it difficult to draw meaningful conclusions about the summer diet. However, previous work on Lake Washington indicated that the majority of the summer diet of cutthroat trout smaller than 350 mm was composed of zooplankton (Beauchamp et al. 1992). Cutthroat trout larger than 350 mm primarily consumed fish, but zooplankton was still important in the diet (Beauchamp et al. 1992). Based on the limited number of samples we collected in summer, our results were generally similar to those of Beauchamp et al. (1992). Between June 21 (late spring) and July 7 (1998 and 1997), we sampled 20 cutthroat trout. Zooplankton made up 71% of the diet of cutthroat trout smaller than 350 mm ($N = 16$). In contrast, 79% of the diet of cutthroat trout larger than 350 mm ($N = 4$) was contributed by fish (threespine sticklebacks and sculpins), but no zooplankton were consumed.

We investigated annual differences in piscivory because the abundance of longfin smelt, a major prey resource, varies greatly between even and odd years (Moulton 1970). We hypothesized that when odd-year spawning classes of longfin smelt were present in Lake Washington as age-1 fish, cutthroat trout would eat more sockeye salmon and other salmonids, because few age-1 longfin smelt would be present and because age-0 longfin smelt would be too small. Consistent with this prediction, more sockeye salmon were consumed when odd-year spawning classes of longfin smelt were present as age-1 fish (i.e., few large smelt were available). Overall, the number of sockeye salmon prey per cutthroat trout stomach was almost five times higher during periods when the odd-year spawning class was present as age-1 fish. Therefore, longfin smelt appear to buffer predation on sockeye salmon. In other sockeye salmon nursery lakes, forage fish species such as the threespine stickleback, pond smelt *Hypomesus olidus*, and pygmy whitefish *Prosopium coulteri* are also believed to buffer predation on juvenile sockeye salmon (Hartman and Burgner 1972).

Implications for the Management of Lake Washington

Eggers et al. (1978) reviewed the Lake Washington fish community and did not list cutthroat trout as one of the 12 most important fish species in the food web. At that time, the species was only a minor component of the lake's community, although abundance estimates for that period are lacking. There is no continuous sampling record for cutthroat trout in the lake, but anecdotal data from counts of cutthroat trout leaving streams to enter the lake (D. Seiler, WDFW, unpublished data) and from research gill-net catches (B. Footen, MIT, unpublished data) imply a large population during recent years. Two factors may have contributed to the ability of this species to thrive in the urbanized streams around Seattle. First, juvenile cutthroat trout may have benefited from the decline in coho salmon and steelhead juveniles that has occurred in urban streams in this basin (Scott et al. 1986; Lucchetti and Fuerstenberg 1993; Fresh 1994). These two species compete with cutthroat trout for food and space in these streams, and their reduced abundance may have allowed the population of cutthroat trout to expand. Second, the increased abundance of prey fish in the lake since the 1970s has provided a food supply for cutthroat trout that is much larger than the supply available in earlier years. The growth rates currently experienced by cutthroat trout may have fueled the productivity of the population, and perhaps also shifted the population from anadromy to an adfluvial life-history pattern.

Based on the large percentage of sockeye salmon in the diet of cutthroat trout, cutthroat trout could account for substantial losses of juvenile sockeye salmon in the Lake Washington system if their population size were sufficiently large. The cutthroat trout now appears to be the dominant predator in the system, where originally it was rare. Northern pikeminnow were once considered the most important keystone predator in the system (Eggers et al. 1978). Potential relationships between cutthroat trout and northern pikeminnow are currently unclear. For example, cutthroat trout predation may have replaced northern pikeminnow predation or added to it; cutthroat trout may even have affected the population size of northern pikeminnow by preying on juveniles. Regardless, the addition of cutthroat trout to the lake has the potential to significantly affect trophic dynamics and sockeye salmon survival, depending on the population size of cutthroat trout. Thus, management of the complex Lake Washington ecosystem will require an accurate population estimate for cutthroat trout and continued monitoring of their abundance. Managers should consider the effects of the cutthroat trout population on sockeye salmon and other components of the ecosystem, such as longfin smelt and zooplankton abundance.

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