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Temporal, Spatial, and Size-Related Foraging of Wild Cutthroat Trout in Lake Washington

Abstract

We documented the feeding behavior of wild cutthroat trout *Oncorhynchus clarki*, a major piscivore, prior to the planned enhancement of juvenile sockeye salmon *Oncorhynchus nerka*, a potential prey species in Lake Washington. Food habits of cutthroat trout changed with body size, season, and time of day. Cutthroat trout ate invertebrates (*Daphnia pulicaria, Neomysis mercedis*, and various insects) until they reached a large enough size (generally when fork length is longer than 250 mm) to capture small fishes. Seasonal changes in the distribution of cutthroat trout corresponded with that of their primary prey, the longfin smelt, *Spirinchus thaleichthys*, when it was available. Juvenile sockeye salmon was a relatively minor constituent of the diet. Cutthroat trout appear to feed primarily in the littoral and upper limnetic zones, and respond to the diel and seasonal diffferences in accessibility of prey in these zones. This suggests that predation on juvenile sockeye salmon by cutthroat trout might increase in response to enhancement measures or to declines in the longfin smelt population.

Introduction

Temporal changes in prey distribution can influence the feeding behavior of a predator. Seasonal shifts in the abundance, availability, or vulnerability of prey are frequently reflected in a predator's diet. The diel feeding chronology of a predator might also be influenced by diel changes in prey distribution which can directly affect prey availability or vulnerability (Eggers 1977, 1978; Clark and Levy 1988). A description of the seasonal, diel, and ontogenetic changes in the food habits of a predator population is essential for determining the mechanisms of predator-prey interactions.

Cutthroat trout, *Oncorhynchus clarki*, are top predators in many lakes in the western United States. Lacustrine populations generally reside in littoral and limnetic habitats, and exploit fish and invertebrates commonly found in these zones (Idyll 1942, Trojnar and Behnke 1974, Andrusak and Northcote 1971, Nilsson and Northcote 1981, Hindar *et al.* 1988, Stables 1989). Little emphasis has been placed on the diel and seasonal variability in food habits of piscivorous cutthroat trout, however. In the present study, we examine temporal and ontogenetic shifts in the food consumed by subadult and adult cutthroat trout in Lake Washington, and relate this variability to temporal changes in the availability and vulnerability of prey.

The Washington Department of Fisheries plans to construct a spawning channel and/or hatchery to enhance the production of sockeye salmon (*Oncorhynchus nerka*) smolts. At maximum capacity, this facility is predicted to produce 110 million fry (Brannon *et al.* 1988) in addition to the natural river production (estimated to average around 30 million fry per year from 1978 to 1983; Beauchamp 1987).

Juvenile sockeye salmon and longfin smelt (*Spirinchus thaleichthys*) are the predominant planktivorous fishes in the limnetic zone of Lake Washington, and both are potentially important prey of cutthroat trout. A fourfold increase of juvenile sockeye salmon would increase their contribution to the limnetic planktivore community and could elicit a functional response (increased rate of predation with increasing prey density; e.g., Peterman and Gatto 1978) by piscivorous cutthroat trout to the juvenile salmon. Therefore, it is important to describe the current spatial-temporal patterns of predation as a reference for comparisons with the patterns from the expected increase in abundance of juvenile sockeye salmon during the enhancement program. Such a shift in prey selection by the piscivore might seriously compromise the desired goals of the enhancement program.

Study Area

Lake Washington is a large (88 km^2), monomictic lake adjacent to the city of Seattle, Washington,

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USA. The lake generally stratifies from April to October with mean (0-20 m) epilimnetic temperatures ranging from 8° to 16-18°. Further description of the lake and its fish community can be found in Beauchamp (1990). We partitioned the lake into five nearshore (0 to 15 m deep) areas and four offshore areas (from surface to bottom in areas deeper than 15 m), along the longitudinal axis of the lake (Figure 1). The Cedar River mouth and a 100 m area extending beyond the slopes of the river delta formed a 2 ha area designated as nearshore area five (Figure 1).

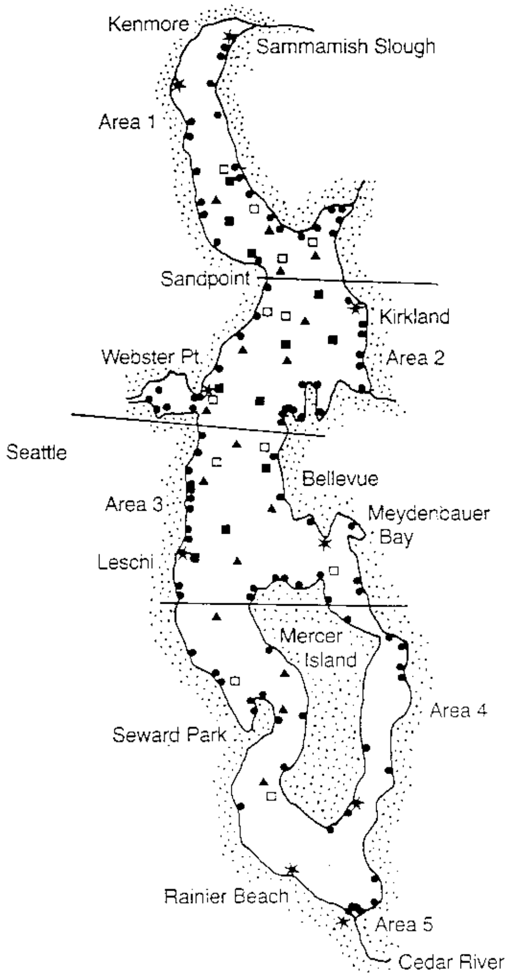

Figure 1. Lake Washington showing the locations sampled in 1984 and 1985. The lake was divided into five areas (delineated by horizontal lines) along its longitudinal axis. The Cedar River delta is area 5. Symbols follow: star, fixed location gill net sets in 1984 and 1985: solid circle, random gillnet sets in 1985; and purse seine sets in May 1985, solid triangle; June 1985, solid square; and September 1985, open square.

Methods

Sampling in the Nearshore Zone

The five nearshore zones were sampled with horizontal gill nets twice each month from January 1984 to June 1985. Two fixed sampling sites within each zone (one each on the east and west sides of the lake) comprised a sampling series in 1984. In 1985, one fixed site and two randomly selected sites were sampled per area during each sampling series. We set gill nets in the nearshore zone 318 times in 1984 and 182 times from January through June, 1985 (Figure 1).

Sinking horizontal gillnets were used for sampling both cutthroat trout and larger prey fish (i.e., yearling and adult longfin smelt, sockeye salmon smolts, yearling yellow perch *Perca flavescens* and peamouth chub *Mylocheilus caurinus*) in the nearshore zones. The nets were 33 m long and consisted of nine panels (3.7 m x 2.0 m) of randomly arranged mesh sizes (25 to 127 mm stretched mesh, in 13 mm increments). The nets were set at 0800-1100 hours and retrieved the next morning. The horizontal gill nets were deployed only in the nearshore zone, and were always set roughly perpendicular to shore. This procedure was repeated until all five areas had been sampled twice each month.

Offshore Zone Sampling

In 1984, we sampled the pelagic predator and prey populations monthly (January to October) in each of the five offshore areas with vertical gillnets. Nine single mesh-sized nets were fished simultaneously in each area for 24 h; the mesh sizes ranged from 25 to 127 mm stretched mesh, and changed in 13 mm increments. Only prey fishes larger than 80 mm were vulnerable to the smallest mesh size we used. We assumed that catches in these nets provided an approximation of the vertical distribution of fishes integrated over the 24 h set time.

Recognizing the limitations of the vertical gillnet data, we sampled with 3-m Isaacs-Kidd midwater trawl at night to document the nocturnal distribution of all sizes of the major pelagic prey fish whenever possible. The trawl was towed at 9.7 km/h for 10 min at depth, and tows were made at depths of 8, 15, 22, 30, 36, and 50 m (bottom depth permitting) in each of the five areas. We recorded the catches of each fish species by tow depth, area, and time. The midwater tows were made in late March or early April in 1984 and 1985 by Washington Department of Fisheries personnel. We were able to do additional midwater trawling in September and November 1987, and November 1988. These latter midwater trawl samples were taken several years after collection of the cutthroat trout stomach samples, but the distribution patterns of prey fishes agreed well with those reported earlier by Dryfoos (1965) and Traynor (1973). Given the consistency of distribution patterns reported over a 22 year period, we felt justified in assuming that the summer and autumn vertical distribution patterns observed in 1987 and 1988 could be applied to the years of our study (1984-1985).

A 17.7 m purse seine vessel was chartered in May, June, and September 1985 to sample predators in the pelagic zone. Serial purse seine samples were collected roughly every hour from 1500 to 0500 hours on 14-16 May, from 1800 to 1100 on 13-14 June, and from 1100 to 2300 on 19 September (Figure 1). A stratified random sampling design was used, with samples proportionally allocated according to the surface area of the pelagic zone in areas 1, 2, 3, and 4. Each vessel deployed a large herring seine (600 m corkline, 37 m deep, 2.5 cm stretch mesh). Each circular set represented one unit of effort and the time at which the seine was pursed was designated as the set time.

Stomach Analysis

Sample sizes from 1984 were small due to our concern for conserving wild, reproductive fish (the population size was not known at the time), and because many of the stomachs, especially from spawning fish sampled in winter were empty (75% in 1984 versus 22% in 1985). However, after discovering that the annual catch of wild cutthroat trout was approximately 20 percent of that for stocked rainbow trout, *Oncorhynchus mykiss*, in our 1984 samples, we analyzed the stomach contents of all trout sampled thereafter. Although trends in the food habits of cutthroat trout were similar during both years, we emphasize the 1985 data here because of the larger sample sizes.

Cutthroat trout captured in purse seines were anesthetized with MS-222, measured, weighed, stomach-pumped, allowed to recover, and then released near the area of capture. Cutthroat trout captured in gillnets were killed to provide stomach samples for analysis of the seasonal nearshore diet composition.

We analyzed stomach contents from all captured cutthroat trout. Fish were measured (fork length to the nearest 1 mm) and weighed (nearest 1 g) before stomach contents were removed. Prey items were categorized as fish (identified to species whenever possible), zooplankton, Mysidacea (*Neomysis mercedis*), insects, and other invertebrates. Lengths of prey fish were measured, and dry weights (20 h at 80 °C) for each prey category were recorded as a proportion of the total weight of stomach contents from each fish.

Results

Predation by cutthroat trout on their major prey changed significantly between nearshore and offshore habitats (Mann-Whitney U test, $P < 0.02$ for fish prey, $P < 0.02$ for zooplankton, and $P < 0.0001$ for insects). Similarly, predation patterns on most major prey varied among seasons (Kruskal-Wallis test, $P < 0.05$ for fish prey, $P < 0.01$ for insects, but $P < 0.15$ for zooplankton). Therefore, we stratified this analysis by season and nearshore and offshore habitat.

Temporal Changes in the Distribution of Cutthroat Trout and Prey

The seasonal nearshore-offshore occurrence of cutthroat trout generally corresponded with the seasonal distributions of its potential prey species. *Daphnia pulicaria* became abundant in the upper 20 m of the epilimnion during May and remained so through early to midsummer; minimum summer densities occurred in August or September, and a second period of high density coincided with thermal destratification in October (W. T. Edmonson, unpublished data). We caught longfin smelt in both nearshore and offshore gillnets during late autumn and winter, but only caught them offshore in spring and summer (Figure 2). The relatively high catches of longfin smelt during winter corresponded to a strong even-numbered year-class that spawned and died, subsequently leaving a weak, odd-numbered year-class of over-yearlings in the lake. Juvenile sockeye salmon occupied the limnetic zone except as fry entering or as smolts leaving the lake (Figure 2). Although cutthroat trout

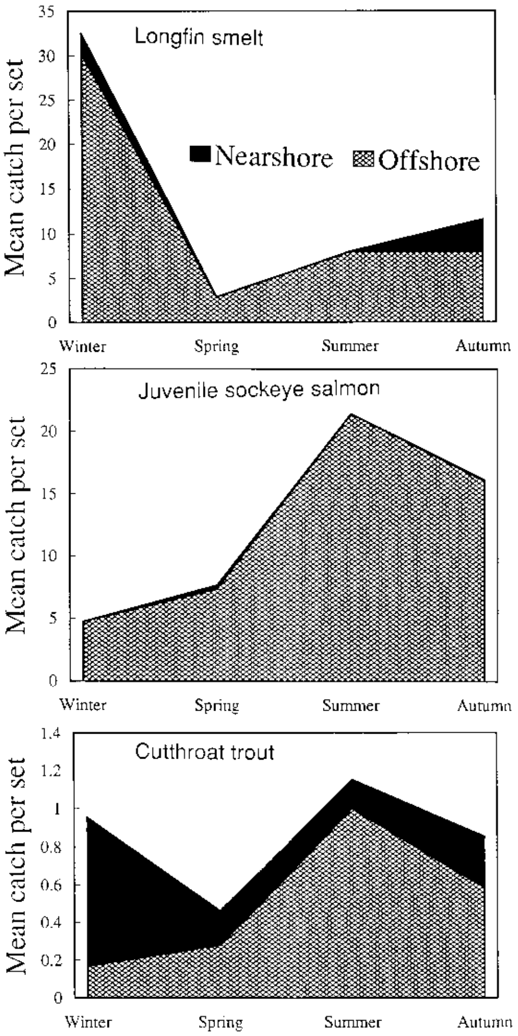

Figure 2. The seasonal nearshore-offshore distribution of longfin smelt, juvenile sockeye salmon, and cutthroat trout as indicated by the seasonal mean catch per set of horizontal gill nets nearshore and vertical gill nets offshore.

occupied both nearshore and offshore habitats throughout the year, more were caught offshore during spring, summer, and autumn, whereas the opposite was true in winter (Figure 2).

The diel vertical distribution of pelagic prey varied among species, but coincided with that of cutthroat trout at various times of the day. Pelagic cutthroat trout were most abundant at depths of 10 to 30 m in spring and summer with 55 percent of the catch between depths of 15 and 20 m both day and night (Figure 3). At night, the spring through autumn (April 1984, 1985; September, November 1987) midwater trawl catch of longfin smelt was highest at 8 m, whereas the catches integrated over 24 h in vertical gillnets indicated that longfin smelt remained deeper during the daylight and crepuscular periods (Figure 3). In contrast, the nocturnal catches of juvenile sockeye salmon were evenly distributed between 10 and 30 m in spring; in summer catches were highest between 22 and 30 m; and in autumn, nocturnal catches were highest between 30 and 50 m (Figure 4). Again, the 24 h vertical gillnet catches of juvenile sockeye salmon suggested that daytime and crepuscular distributions were generally deeper than those at night (Figure 4).

Food Habits in the Nearshore Zone

Winter-spring—Small cutthroat trout (150-250 mm) ate mostly invertebrates during winter and spring, whereas larger cutthroat trout ate mostly fish (Figure 5). The primary prey of small cutthroat trout was insects (mostly larval and pupal chironomids) during winter, and mysids and *Daphnia pulicaria* in spring. During both winters, large cutthroat trout fed primarily on longfin smelt and to a lesser extent on prickly sculpin *Cottus asper* (Table 1). In 1984, large cutthroat trout ate significantly more longfin smelt in winter (Kruskal-Wallis test, $P < 0.05$) when larger numbers of spawning adult longfin smelt were available than in spring (Table 1). When the spawning population of longfin smelt was small in 1985, there was no significant difference in the number of immature yearling longfin smelt eaten between winter and spring (Kruskal-Wallis test $P > 0.2$). A small number of juvenile sockeye salmon and yellow perch were found in the stomachs of large cutthroat trout during winter and spring in 1985 (Table 1).

Summer—Cutthroat trout shorter than 300 mm ate insects, *Daphnia pulicaria*, and mysids during summer in the nearshore zone. Larger cutthroat trout ate mostly fish, including juvenile sockeye salmon (24% of the stomach contents by dry weight), threespine stickleback *Gasterosteus aculeatus* (25%), and longfin smelt (1%; Table 1).

Food Habits in the Offshore Zone

During spring and summer, fewer *Daphnia pulicaria* (Kruskal-Wallis test, $P < 0.0001$) and more longfin smelt and total fish ($P < 0.01$ and

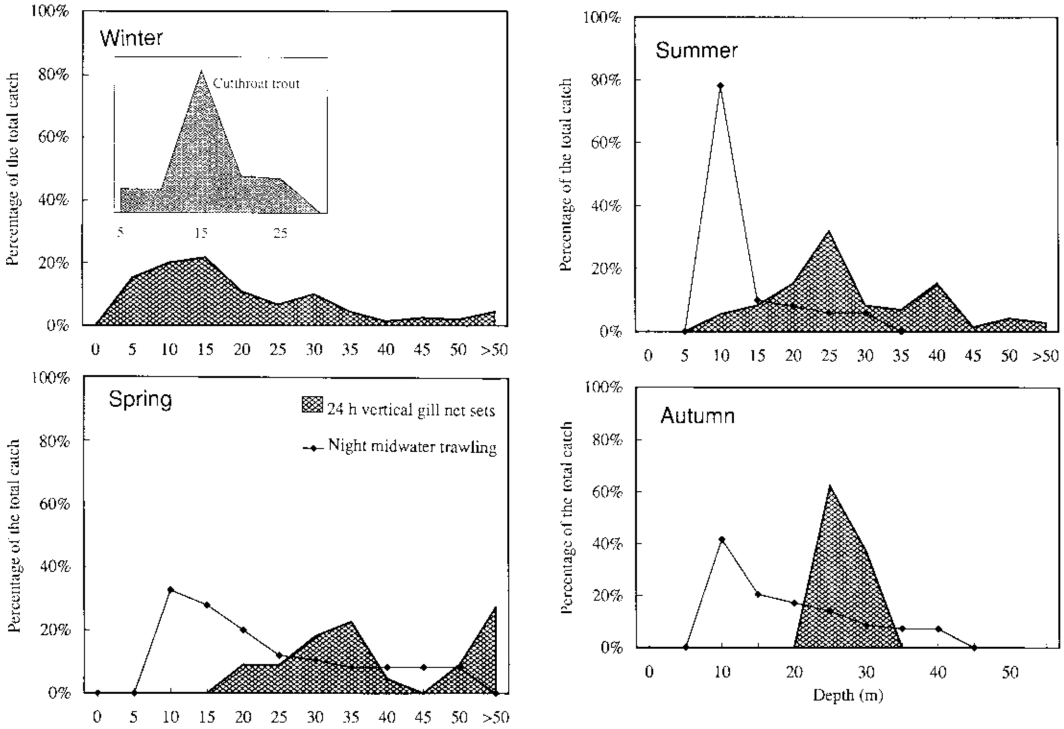

Figure 3. The diel vertical distribution of pelagic longfin smelt during winter, spring, summer, and autumn as inferred by the difference in depth distribution of the catches from vertical gill nets set for 24 h (1983-1985), and from midwater trawling at night (April 1984, 1985, September and November 1987, November 1988, and July 1989). The vertical distribution of pelagic cutthroat trout all year is indicated by the inset (depth scale of 5-30 m) in the top left panel.

TABLE 1. Percentage composition (by dry weight) of prey fish species in the diet of large (≥250 mm) cutthroat trout by season and habitat in Lake Washington. Species in the Other Fish column are identified as L = larval fish, S = juvenile coho or chinook salmon, Y = yellow perch, and are ordered from highest to lowest proportion of the stomach contents by dry weight.

Length Category (mm)	N	Longfin Smelt	Sockeye Salmon	Threespine Stickleback	Prickly Sculpin	Other Fish	Unidentified Fish
Winter 1984, Nearshore							
≥250	8	60	0	0	2	0	13
Spring 1984, Nearshore							
≥250	10	10	0	6	0	0	10
Summer 1984, Nearshore							
≥250	4	1	24	25	0	0	0
Summer 1984, Offshore							
≥250	4	0	23	9	0	16	25
Winter 1985, Nearshore							
≥250	28	24	2	0	4	4	36
Spring 1985, Nearshore							
≥250	37	8	2	0	1	5	21
Spring 1985, Offshore							
250-299	6	11	0	0	0	17 L	0
≥300	40	55	2	2	0	9 Y, S, L	14
Summer 1985, Offshore							
250-299	24	4	0	6	0	0	11
≥300	33	12	10	16	3	0	26

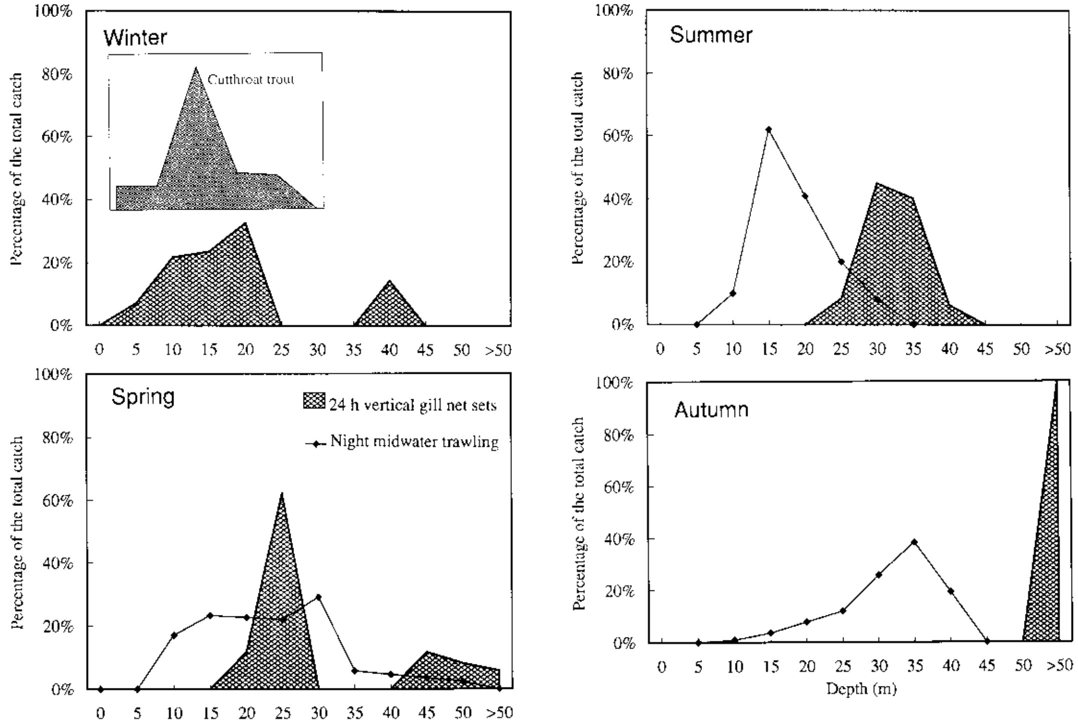

Figure 4. The diel vertical distribution of pelagic juvenile sockeye salmon during winter, spring, summer, and autumn as inferred by the difference in depth distribution of the catches from vertical gill nets set for 24 h (1983-1985), and from midwater trawling at night (April 1984, 1985, September and November 1987, November 1988, and July 1989). The vertical distribution of pelagic cutthroat trout all year is indicated by the inset (depth scale of 5-30 m) in the top left panel.

0.0001, respectively) were eaten as the size of cutthroat trout increased (Figure 5). During spring, cutthroat trout longer than 300 mm ate fish, primarily longfin smelt (Table 1), whereas *Daphnia pulicaria* and insects comprised less than a third of the diet (Figure 5). In summer, fish were still the predominant prey of cutthroat trout larger than 350 mm, whereas the contribution of daphnids in the diet declined with increasing predator size, and insects became a minor component of the diet (Figure 5). Threespine stickleback was the most important fish prey of large cutthroat trout in summer, followed by longfin smelt, prickly sculpin, and juvenile sockeye salmon (Table 1).

Diel Feeding Patterns of Pelagic Cutthroat Trout

The prey of pelagic cutthroat trout varied with time of day during spring and summer (Kruskal-Wallis test: $P < 0.005$ for longfin smelt, $P < 0.005$ for *Daphnia pulicaria*, and $P < 0.05$ for total fish prey; Figure 6). The weight of longfin smelt in the stomachs of cutthroat trout was greatest about 2 h after both sunrise and sunset, whereas the amounts of *Daphnia pulicaria* and juvenile sockeye salmon eaten were highest during daylight. The digestive state (He 1991) of the longfin smelt (bodies intact, some with small patches of skin missing) recovered from the peak feeding periods indicated that ingestion had occurred 0-2 h (at 15°to 17°) before the cutthroat trout were captured. Threespine stickleback were eaten both day and night.

Predator and Prey Fish Size

The size of fish eaten by cutthroat trout varied by season and species of prey ($P < 0.001$; two-way ANOVA; Table 2). Correlations between predator size and fish prey size were generally not significant except during the summer when the size of ingested longfin smelt showed a strong positive correlation with predator size ($r = 0.94$, $P < 0.02$; Figure 7). The size of threespine stickleback eaten showed a weak, but significant positive correlation

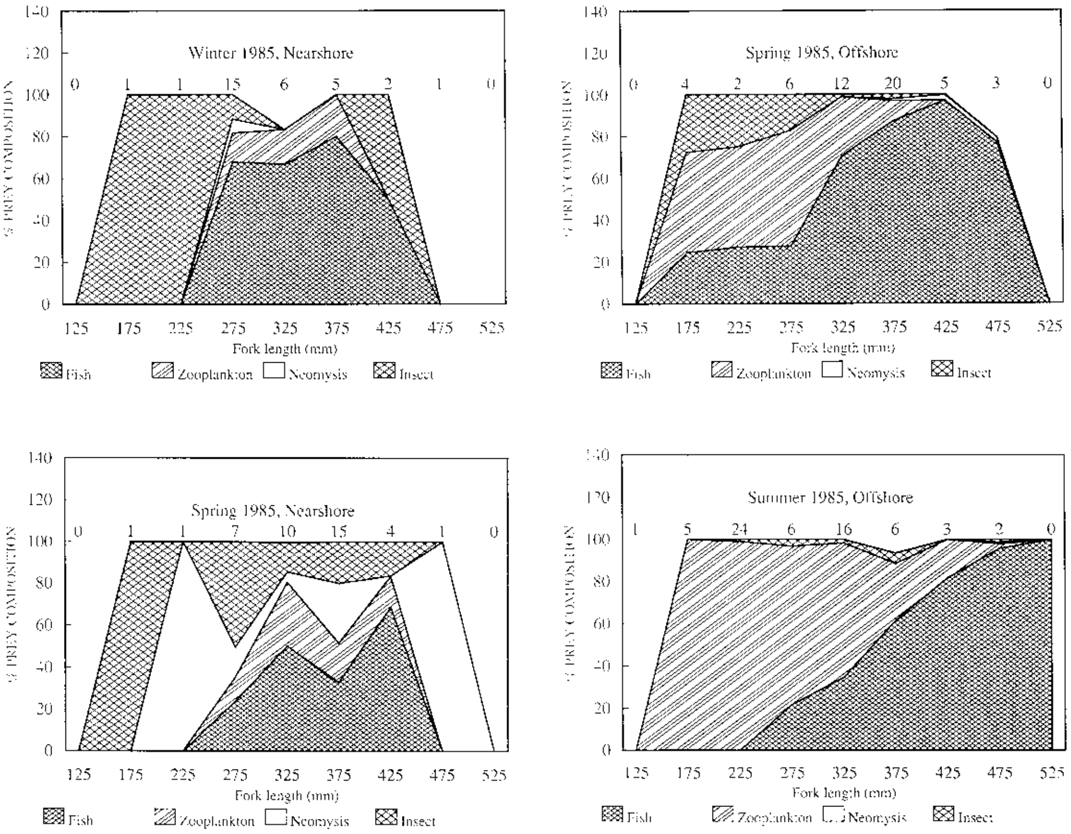

Figure 5. Percentage composition (dry weight) of fish, zooplankton (*Daphnia pulicaria*), mysids (*Neomysis mercedis*), and insects in the diet of all sizes of cutthroat trout in the nearshore areas during winter and spring 1985, and offshore during spring and summer 1985. Numbers indicate sample size for each 50 mm length interval.

TABLE 2. The mean length and SE of fish eaten by cutthroat trout during different seasons in Lake Washington.

Prey Species	n	Mean Fork Length	SE
Winter			
Longfin smelt	18	103	9
Prickly sculpin	3	83	1
Spring			
Longfin smelt	145	57	1
Prickly sculpin	3	29	1
Yellow perch	6	73	5
Sockeye salmon	37	26	1
Summer			
Longfin smelt	11	69	5
Prickly sculpin	31	37	2
Sockeye salmon	14	64	2
Threespine stickleback	71	36	1

with predator size ($r = 0.24$, $P < 0.05$), whereas size of the juvenile sockeye salmon eaten was not related to predator size ($r = 0.05$).

Discussion

The diet of cutthroat trout changed with body size, season, and time of day. Cutthroat trout ate invertebrates until they were large enough (generally larger than 250 mm) to routinely capture small fishes such as longfin smelt, threespine stickleback, prickly sculpin, and juvenile sockeye salmon. Luecke (1986) described ontogenetic shifts in the food of juvenile cutthroat trout in Lake Lenore, Washington, from zooplankton to larger benthic invertebrates, when the fish attained a length of 70 mm. Juvenile cutthroat trout in the Lake Washington drainage were generally 134-175 mm long before migrating from the natal stream into the lake (Scott *et al.* 1986). Hence, even the smallest

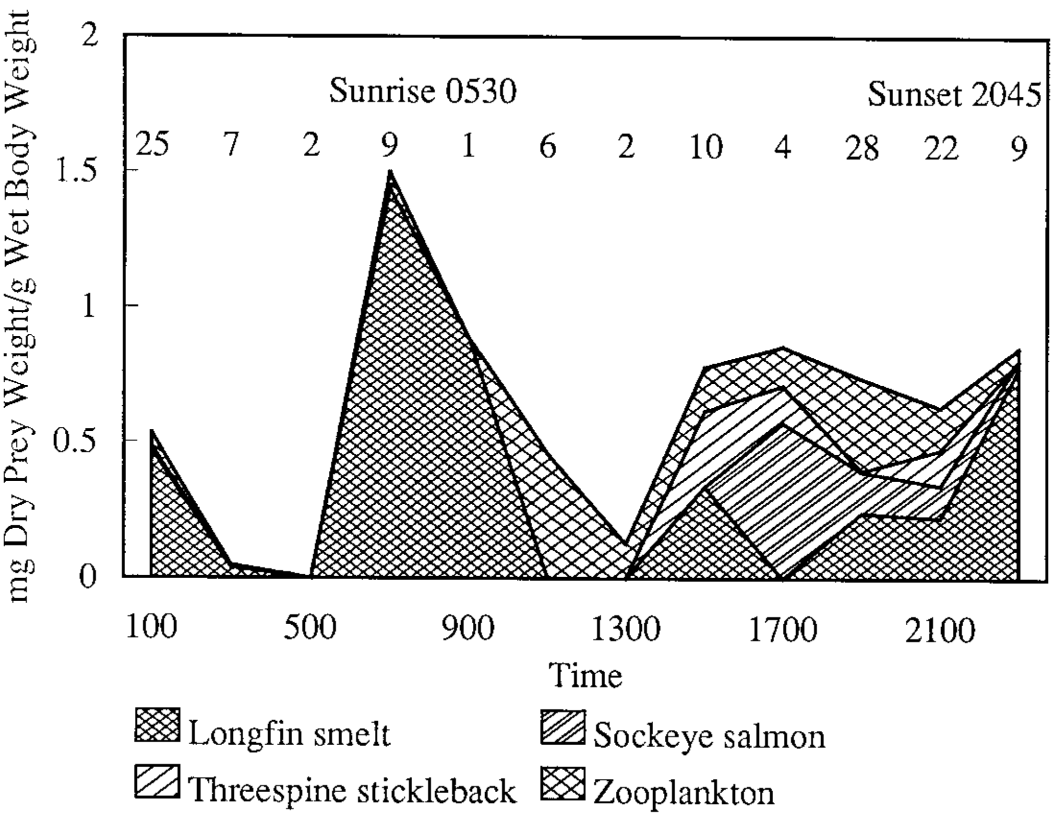

Figure 6. Diel consumption of major prey by cutthroat trout in the offshore zone of Lake Washington during May, June, and September 1985. Numbers indicate the sample size for each 2 h interval.

lacustrine cutthroat trout could utilize both zooplankton and other invertebrates (e.g., mysids and insects). When both invertebrate and fish prey are available, larger cutthroat trout could select zooplankton, benthic invertebrates, or fish. Shifts in prey composition might also be mediated by temporal changes in prey abundance and availability.

Longfin smelt was the primary prey of large cutthroat trout, as their distributions coincided throughout the year. Cutthroat trout occupied shallow to intermediate depths in the limnetic and littoral areas from spring through autumn, and concentrated more in the littoral zone at shallow to intermediate depths in winter. Longfin smelt occupied the pelagic zone from mid-spring through autumn; some longfin smelt resided in the limnetic zone in winter, but most moved to nearshore or profundal habitats (Traynor 1973, Beauchamp 1987). The nearshore prey community is in a state of flux during spring: adult longfin smelt die after spawning in winter (Dryfoos 1965), yearlings move offshore in mid-spring as the *Daphnia* populations increase, and warmwater fishes migrate shoreward. The cutthroat trout that remained in the nearshore habitat ate fewer longfin smelt, more invertebrates (particularly *Neomysis mercedis*), and other fishes (e.g., yellow perch). However, most cutthroat trout appeared to move offshore in spring and continued feeding on longfin smelt.

Longfin smelt populations exhibit cyclic patterns of abundance (Dryfoos 1965, Moulton 1974), wherein even-numbered year-classes are typically 5 to 15 times more abundant than odd-numbered year-classes (Beauchamp 1987). Longfin smelt mature in 2 yr, spawn, and then die shortly thereafter (Dryfoos 1965); hence, this alternating cycle of low and high abundance is maintained. Although few cutthroat trout were sampled in 1984 when the abundance of longfin smelt was low, the data suggested that juvenile sockeye salmon became the predominant prey during the summer.

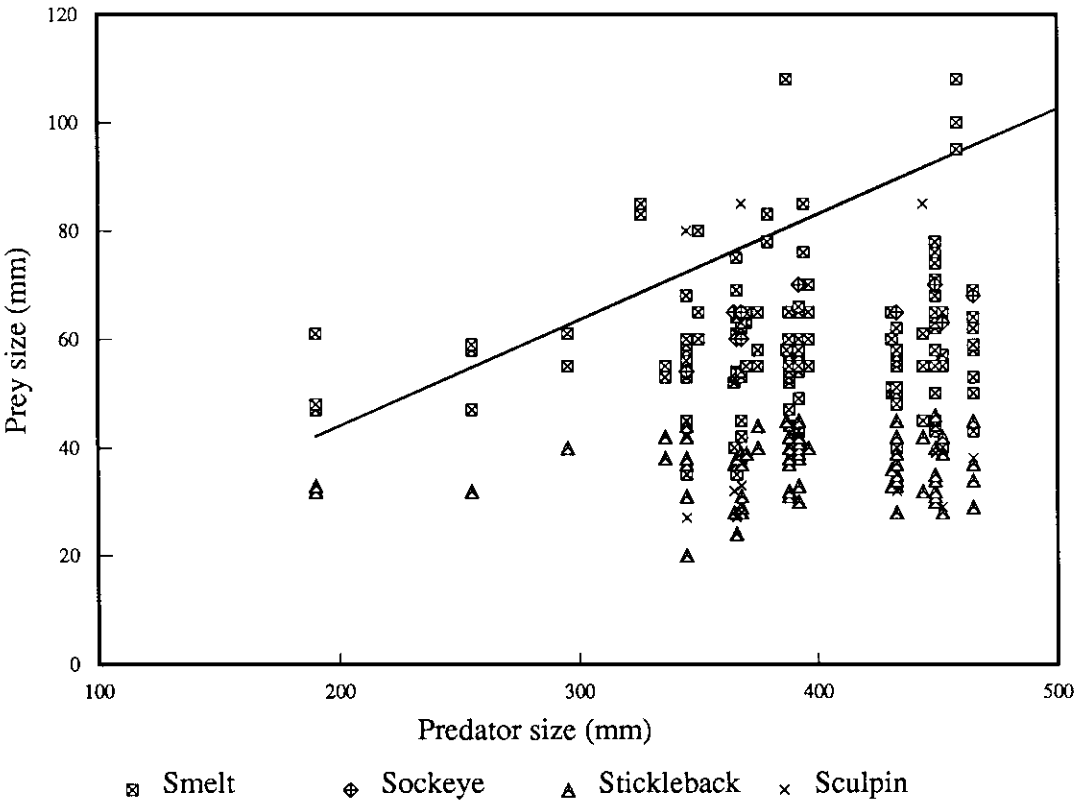

Figure 7. The relationship of predator size to prey size, pooled for all prey species and all seasons. The line indicates the only strong relationship which was between the size of piscivorous cutthroat trout and longfin smelt prey during the summer: (prey length) = 5.060 + 0.195 × (piscivore length), $r^2 = 0.86$, $N = 7$.

The diel pattern of predation by pelagic cutthroat trout on different prey corresponded with temporal changes in the vertical distribution or visibility of prey. Daphnids were abundant in the top 20 m of the water column during late spring, summer, and autumn (Edmondson and Litt 1982), and were eaten during daylight. Longfin smelt, which stay in deep water habitat during the day (Dryfoos 1965) were eaten during the crepuscular periods. Longfin smelt must pass through the depths occupied by cutthroat trout to feed in the upper epilimnion where uplooking predators benefit from the contrast between the silhouette of their prey and backlighting from the twilight sky.

When small planktivorous fishes occupy the lighted upper water column, they are vulnerable to sight-feeding predators (Eggers 1978, Beauchamp 1987, Clark and Levy 1988). Although we did not collect data on daytime distributions of pelagic prey fish, the differences between our vertical gillnet catches which integrated over 24 h periods and the discrete night-time trawl samples from later years are suggestive of the patterns observed by others. Dryfoos (1965) found that the median depth of yearling longfin smelt was 8 to 20 m deeper during the day than at night in summer and autumn. Eggers (1978) reported that individual juvenile sockeye salmon generally remained deeper than 40 m during the day, whereas those in schools foraged between depths of 10 and 30 m in summer and autumn. Threespine stickleback were rarely caught in midwater trawls during summer and autumn, but were often observed at the surface associated with floating mats of aquatic macrophytes and other debris in the pelagic zone.

Juvenile sockeye salmon were eaten only during daylight by pelagic cutthroat trout, but threespine stickleback were eaten during both day and night. During daylight, juvenile sockeye salmon in Lake Washington remain in the deep limnetic zone or forage at intermediate depths using schooling as an antipredation strategy (Eggers 1978). Cutthroat trout might be able to locate schools of juvenile sockeye salmon at intermediate depths during the day when there is sufficient light for both piscivore and planktivore to locate their prey. Schooling behavior of juvenile sockeye salmon suggests that they are vulnerable to predation at these depths and times. The schools disperse at dusk when individuals might be less susceptible to predation than longfin smelt, which move higher in the water column.

The light threshold above which cutthroat trout can detect prey of a certain size probably influences their vertical distribution, and in turn, influences their diel shift in prey composition. Cutthroat trout in Loon Lake, British Columbia, could detect the copepod *Diaptomus kenai* (1.4-1.6 mm) below 30 m during daylight, but could not do so even at the surface between dusk and dawn; the sympatric Dolly Varden (*Salvelinus malma*) could still detect zooplankton all night between 5 m and the surface (Henderson and Northcote 1985). Inasmuch as the transparency of Lake Washington (Secchi disk transparency = 7 m) was slightly less than that of Loon Lake (8 m) in summer, the maximum depth of prey detection in Lake Washington would also be less. Cutthroat trout in the upper 20 m could feed on zooplankton during the day, and still have sufficient light to feed on larger prey like longfin smelt (50-130 mm) at dusk and dawn, when zooplankton were no longer detectable. Juvenile sockeye salmon would certainly be detectable in schools foraging at depths of 10 to 30 m (Eggers 1978) in daylight, but not when individuals were dispersed in deeper water. Since pelagic threespine stickleback appeared to remain near the surface, associated with floating cover, during summer and autumn, they would be vulnerable to predation by cutthroat trout at all times, and indeed were eaten both day and night.

An understanding of the spatial and temporal aspects of predator-prey interactions should help identify potential mechanisms of prey selection, and assist in identifying potential prey switching by cutthroat trout in response to the sockeye salmon enhancement plan. Our examination of the current foraging behavior of cutthroat trout will provide a valuable reference to compare to the predator-prey interactions during the enhancement program. The potential for predators to switch to the commercially and recreationally desirable sockeye salmon during years of low longfin smelt abundance has important implications for managing the fish community in Lake Washington. If a dramatic increase in the abundance of juvenile sockeye salmon, relative to longfin smelt and threespine stickleback, causes predators to feed selectively rather than opportunistically on sockeye salmon, then the resulting increased predation could seriously reduce the benefits expected from enhancing the sockeye salmon population.

Acknowledgments

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