

Spatial–Temporal Dynamics of Early Feeding Demand and Food Supply for Sockeye Salmon Fry in Lake Washington

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Abstract.—We compared temporal consumption rates by sockeye salmon *Oncorhynchus nerka* fry with food supply to evaluate how different survival and dispersal rates or additional hatchery production affected the winter carrying capacity of Lake Washington, Washington. Peak immigration of sockeye salmon fry into southern Lake Washington precedes the spring zooplankton bloom by 2–3 months. Zooplankton density, fish diet, and growth were sampled during winter and spring 2001, when a record 52.4 million fry entered the lake. Supplementary information on the distribution and dispersal of fry was collected in 2002 and 2003. We used bioenergetics modeling to estimate the temporal–spatial consumption by fry during early lake rearing. *Cyclops bicuspidatus* were dominant in the diet and zooplankton assemblage but declined from more than 30/L in late February and early March to fewer than 5/L during mid-March and early April. Fry ate significantly larger *Cyclops* than the average size in the lake; approximately 83% of the food items in the stomachs were larger than 0.8 mm, which was the minimum food item size. Hydroacoustics and midwater trawling surveys during 2002 and 2003 suggested that fry dispersed quickly over the southern half of the lake and used depths of 0–30 m. Under the most realistic scenarios for fry dispersal, feeding, and survival, total consumption of all prey by sockeye salmon fry represented 5% of the average monthly biomass of *Cyclops* during March and early April, when their availability was lowest. Potential bottlenecks in the availability of *Cyclops* only developed in simulations when fry were restricted to feeding in 0–10-m depths in the southernmost region of the lake. Despite the seemingly adequate food supply for sockeye salmon fry, other planktivores also consume significant fractions of the exploitable prey biomass, and the interannual availability of exploitable zooplankton varies considerably during winter and early spring. Either of these factors could impinge on the localized food supply for sockeye salmon and other species during some years and should be considered in the adaptive management of any enhancement program.

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Successful recruitment depends on a sufficient supply of food and favorable environmental conditions during the early life history of fish (Cushing 1990). Postlarval fish contain minimal energy reserves after yolk absorption, so timing of entry into the rearing environment should coincide with the presence of an adequate biomass of prey. If a temporal or spatial mismatch exists between the distributions of prey and consumers (Chick and van den Avyle 1999; Plaganyi et al. 2000), those prey that are actually accessible to the consumers may represent a relatively small fraction of the

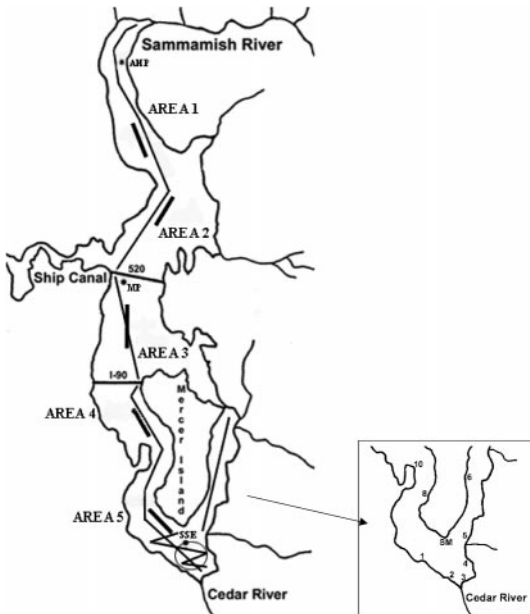


FIGURE 1.—Map of Lake Washington in the Seattle, Washington, area. Borders of sampling areas 1–5 are depicted. Floating bridges form the northern (Highway 520 bridge) and southern (Interstate 90) boundaries of area 3. Midwater trawling locations in area 5 (March 29, 2001) and area 2 (May 8, 2001) and areas 1–5 (March 24–28, 2003) are indicated by dark line segments; surface trawling in March–April 2001 occurred throughout the circled region south of Mercer Island; hydroacoustic transects (February–April 2002) are indicated by the lighter lines that zigzag through all five areas; and routine daylight zooplankton sampling sites are shown as dots labeled AHP, MP, and SSE. Sites used for nocturnal beach seining and day–night zooplankton sampling (sites 1–10 and SM) in southern Lake Washington (inset).

total prey biomass, and starvation could ensue, despite a seemingly adequate supply of food. Increasing the abundance of consumers could exacerbate the effects of such a mismatch either immediately or by creating a delayed bottleneck in food supply for later life stages (Bollens et al. 1992; Rieman and Myers 1992). For sockeye salmon *Oncorhynchus nerka*, which often begin lake-rearing before spring zooplankton blooms (Burgner 1991), such concerns become paramount when considering enhancement programs.

Lake Washington currently supports the largest population of sockeye salmon in Washington (Brannon et al. 2001). Most spawning and fry production occur in 37 km of the Cedar River from Landsburg Dam downstream to the southern end of Lake Washington (Figure 1); a smaller fraction

of adults spawn in tributaries to the Sammamish River at the north end of the lake, most notably Bear Creek. In response to a strong negative correlation between peak stream discharge and incubation survival in the Cedar River (Stober and Hamalainen 1980; Thorne and Ames 1987; Seiler et al. 2001), a temporary sockeye salmon hatchery on the Cedar River was established in 1991 and has operated through the 1990s. Its production capacity is up to 17 million unfed fry per year. A permanent mitigation hatchery has been proposed to replace the temporary hatchery and would have the capacity to produce up to 34 million unfed sockeye salmon fry annually (Brannon et al. 2001). Its purpose is to mitigate for the estimated additional fry production that could have been realized if spawning were allowed above Landsburg Dam and to reduce the high interannual variability in fry recruitment. This proposed expansion raised concern that the additional fry production might create localized mismatches between fry and their zooplankton prey in southern Lake Washington when fry enter the lake in late winter.

Naturally produced sockeye salmon fry in the Cedar River and other tributaries emerge and generally migrate at night to Lake Washington during January through May. Peak migration is highly protracted, continuing from mid-February through April. From 1992 to 2000, total annual recruitment of 5.9–38.3 million sockeye salmon fry entered the southern end of the lake, with annual hatchery contributions of 1.4–13.9 million fry and natural production of 0.7–27.4 million fry (Seiler et al. 2001; D. Seiler, unpublished data). Most juvenile sockeye salmon live in the lake for a year and emigrate to sea the following May; however, some juveniles become smolts and migrate to sea in July of their first year after just 5–6 months of growth in the lake (D. Seiler and K. Fresh, unpublished data).

Sockeye salmon fry play an important role in the planktivore community in Lake Washington. Although juvenile sockeye salmon feed heavily and preferentially on *Daphnia* spp. when available, most newly-emerged fry enter the lake 1–3 months before the *Daphnia* population blooms in mid-May. Earlier modeling of the major planktivores was conducted before seasonal diet data were available for the key planktivorous species; consequently, *Daphnia* were conservatively assumed to be the only zooplankton utilized. These simulations indicated that the combined consumption by zooplanktivorous fishes (Beauchamp 1996) and freshwater shrimp *Neomysis mercedis* (Beau-

champ, unpublished data) accounted for less than 10% of the average monthly biomass of *Daphnia* during April through November. However, planktivore consumption would have seriously exceeded food supply during winter and early spring unless alternatives to *Daphnia* were included in the diet. The previous analysis established that juvenile sockeye salmon and mysids were the most important zooplankton consumers during winter, but actual diet composition during winter and spring was unknown. Also, the spatial and temporal dynamics of prey supply and demand were not known. Thus, additional information was needed on the diet composition of sockeye salmon and the temporal-spatial availability of their prey during this potentially critical period when fry first enter the lake.

The purpose of this study was to examine the availability of prey relative to the consumption demand of age-0 sockeye salmon (hereafter referred to as fry) during their first months after entry into Lake Washington from the Cedar River. Specifically, we asked whether food limitation occurred in time or space due to the distribution and feeding patterns of fry or the abundance and distribution of prey. The winter-spring period of 2001 provided a particularly good opportunity to address this question because large spawning escapements in 2000 and unusually benign incubation conditions in the Cedar River (absence of flooding during egg and alevin stages) combined to produce the highest recorded population of fry entering the southern end of Lake Washington (52.4 million: 38.3 wild fry and 13.9 hatchery fry) in 2001. The new hatchery could release up to 34 million fry through the upper, middle, and lower reaches of the river below Landsburg Dam. Survival of migrating hatchery fry varies from less than 10% to nearly 100%, depending on stream discharge rates and distance from release site to the lake (Seiler et al. 2001), so the actual abundance of hatchery fry entering the lake would be considerably lower than 34 million. If, under rare circumstances, high natural spawning escapement corresponded with exceptionally high survival during incubation and emigration, a maximum of 72 million fry (34 million hatchery fry and 38 million wild fry) might theoretically occur. This provides a useful upper limit that is about 40% higher than the abundance of fry observed during our study; the 52.4 million fry entering the lake in 2001 represents a more reasonable expectation of total hatchery and wild fry recruitment to the

lake under the proposed mitigation hatchery regime.

Because fry recruitment during 2001 was comparable to the abundance of fry expected under the proposed enhancement program, a unique opportunity arose to examine the potential carrying capacity of the ecosystem for sockeye salmon fry. Because high densities of sockeye salmon fry entered the southern end of the lake when zooplankton biomass was at the lowest level for the year, we evaluated whether the localized food supply became limiting at any time from winter to mid-May when *Daphnia* densities increase. Our objectives were to (1) estimate the temporal-spatial availability of the major crustacean zooplankton during winter through mid-May, the period of fry immigration to the lake and residence before the annual *Daphnia* increase; (2) estimate the diet and distribution patterns of sockeye salmon fry during the initial months after lake entry; (3) estimate the temporal consumption demand by sockeye salmon fry on their primary prey under different habitat use scenarios; and (4) compare the temporal-spatial consumption demand to prey supply under different fry survival and dispersal scenarios. In this paper, we first constructed a nominal consumption demand scenario for sockeye salmon fry based on the annual survival rate, growth, and diet patterns estimated from 2001. These patterns suggested that fry initially used the near-surface layer in both nearshore and offshore habitats but shifted quickly to an exclusively offshore existence. Consumption demand estimates were also compared among the nominal simulations and alternative habitat use scenarios, which assumed either exclusive nearshore use, exclusive offshore use, or combined use of nearshore and offshore habitats. The fry distribution and dispersal patterns observed during 2002 and 2003 were combined with the nominal consumption demand scenario from 2001 and the temporal-spatial pattern of edible zooplankton biomass during 2001 to compare monthly estimates of prey supply and demand. We then explored the sensitivity of the supply and demand comparisons under different fry survival rates (4–100% annual survival), fry dispersal, and habitat use scenarios. Dispersal scenarios ranged from a highly concentrated population confined to the upper water column in the southernmost region of the lake to the more broadly dispersed patterns observed during 2002 and 2003.

Study Site

Lake Washington is a large, glacially-formed urban lake that drains into Puget Sound in western

Washington. Its large size and proximity to Seattle make it a popular recreational area with significant fisheries. The lake is 32.2 km long, averages 2.5 km wide; its maximum depth is 66 m. Thermal stratification persists from May through October. Surface temperatures ranged from 7.7°C to 23.6°C during 2001, and bottom temperatures (60 m) ranged from 7.5°C to 8.4°C (King County Water and Land Resources Department, unpublished data). Dissolved oxygen levels during our study remained at 5 mg/L or more throughout the water column, except in some years during August–November when levels of 3–5 mg/L were recorded at 50–60-m depths. The lake empties into Puget Sound via the Lake Washington ship canal and the Hiram M. Chittenden locks, where lake surface elevation is controlled (Figure 1).

The primary crustacean zooplankton species in the lake include the cladoceran *Daphnia pulicaria* and the copepods *Cyclops bicuspidatus*, *Diaptomus ashlandi*, and *Epischura nevadensis*. *Daphnia* typically achieve moderate to high densities (5–35 organisms/L) from mid-May through November but are often below detection levels during winter and early spring. Copepod densities during winter and early spring are highly variable among years, either *Cyclops* or *Diaptomus* predominating in the zooplankton assemblage (4–30 organisms/L for the predominant species; Shepherd et al. 2000).

The fish community of Lake Washington has been highly altered from its native condition. The primary zooplanktivores in the lake are juvenile sockeye salmon, other juvenile salmonids (cutthroat trout *O. clarki*, rainbow trout *O. mykiss*, Chinook salmon *O. tshawytscha*, and coho salmon *O. kisutch*), longfin smelt *Spirinchus thaleichthys*, threespine stickleback *Gasterosteus aculeatus*, nonnative juvenile yellow perch *Perca flavescens*, and the freshwater shrimp *Neomysis mercedis*. The primary piscivores include the native cutthroat trout, northern pikeminnow *Ptychocheilus oregonensis*, and prickly sculpin *Cottus asper*, and nonnative resident rainbow trout, adult yellow perch, smallmouth bass *Micropterus dolomieu*, and largemouth bass *M. salmoides*. The vast majority of sockeye salmon fry immigrate from the Cedar River into the southern end of the lake. The Sammamish River contributes a much smaller but significant number of fry entering at the north end, and minor contributions of fry come from smaller tributaries and limited lake spawning.

Methods

We combined field data with bioenergetics modeling to determine whether a mismatch existed be-

tween prey supply and consumption demand by sockeye salmon fry entering the southern end of Lake Washington from the Cedar River. Sockeye salmon fry and zooplankton were sampled from the southern end of Lake Washington from February through May 2001 to determine the growth, diet, and distribution of fry in nearshore and offshore habitats and the availability of their primary prey during the critical first months after immigration to the lake.

The most common growth, diet, and habitat use pattern for newly entering fry (rapid transition from surface-oriented nearshore or offshore habitats to an offshore distribution in the mid to upper water column) was coded into a nominal model simulation to estimate consumption demand on each prey group through time. Monthly population consumption rates on major prey were estimated and compared with the exploitable biomass of the primary zooplankton prey. Three alternative habitat use scenarios were also simulated and incorporated diet and growth patterns associated with (1) an exclusively offshore distribution pattern, (2) an exclusively nearshore distribution pattern, and (3) a combined nearshore–offshore distribution pattern that averaged the temporal growth and diet patterns of the other two scenarios. Simulated monthly consumption rates on key prey were compared among nominal and alternative habitat use scenarios to evaluate the sensitivity of consumption demand to different habitat use patterns.

From the nominal simulation, monthly consumption by fry was compared with the biomass of exploitable prey (based on the size and species composition of prey found in stomach contents) to determine whether food supply could satisfy demand by sockeye salmon fry given the dispersal patterns of fry observed in two subsequent years. The nominal consumption demand was also compared with food supply under different fry survival and dispersal scenarios. We simulated more restrictive fry dispersal patterns by confining the same level of consumption to fewer areas and shallower depths in the southern region of Lake Washington. These comparisons were designed to examine the sensitivity of food demand: supply ratios to potential interannual variability in dispersal or recruitment of wild and hatchery fry.

Zooplankton Data

Day and night zooplankton samples were collected during three periods corresponding with nearshore and offshore sampling for sockeye salmon fry: late February to early March, late March,

and mid-April. Zooplankton samples were collected in vertical hauls via a conical net (1 m long, 0.3 m in diameter, with 153- μm mesh) in nearshore (depth, 0–10 m) associated with nine beach seining sites. Paired day and night offshore zooplankton samples were also collected in 0–20-m vertical hauls offshore of stations 1, 4, and 10 (Figure 1). These samples were compared with zooplankton samples available from routine daylight samples taken at 14-d intervals by University of Washington Department of Biology. Both data sources generated very similar results, so we used the department's data because they represented a long-term, consistent database (Edmondson and Litt 1982; Edmondson 1991) facilitating future comparisons. These samples were collected over discrete depth intervals (0–10 m, 10–20 m, and >20 m) with a 153- μm -mesh Clarke-Bumpus sampler at fixed limnetic stations in the northern (Arrowhead Point [AHP]), central (Madison Park [MP]), and southern (South of South End [SSE]) regions of the lake (Figure 1). Samples were preserved in 95% ethanol until processed in the laboratory. Crustacean zooplankton (cladocerans and copepods) were counted at species resolution and converted to density estimates (organisms/L), assuming 100% net efficiency. Size frequency distributions were generated (via NIH image analysis software) from a subsample of each major species measured with a video camera linked to a dissecting scope. The total biomass of major prey and the biomass of prey that exceeded a minimum edible size threshold (as determined from the size distribution of prey in stomach samples) were estimated for areas 3–5 in the lake by extrapolating size-specific densities of the major prey over the estimated water volumes within the 0–10 m, 10–20 m, and 20–30 m depth intervals.

Fish Data

Fry migration timing and abundance.—Fry migration was quantified by applying a flow-based capture efficiency model (Seiler et al. 2001) to daily fry catches in an inclined plane trap near the mouth of the Cedar River. An estimated 52.4 million sockeye salmon fry migrated from the Cedar River to the lake from January through May 2001, broadly peaking from mid-February to late March (Figure 2). Over 12 million (87%) of the 14 million hatchery fry entered the lake before mid-March, whereas only 22 million (61%) of the 38 million naturally spawned fry had entered the lake by then. For fry entering the lake in 2001, we estimated the survival rate from age 0 to age 1 at 4% (based on

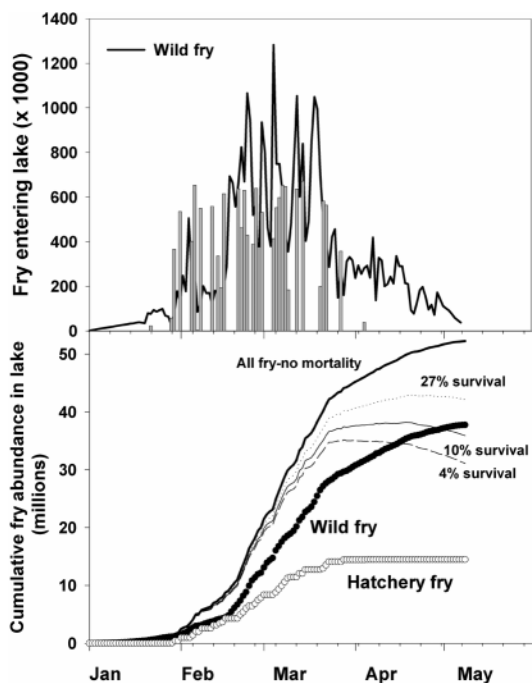


FIGURE 2.—Estimated daily migration (upper panel) of wild (line) and hatchery (gray bars) sockeye salmon fry from the Cedar River into southern Lake Washington, Washington, during 2001. The cumulative abundances of wild and hatchery fry in the lake are shown in the lower panel, along with the total cumulative fry under scenarios of no mortality and annual survival rates of 27, 10, and 4%. Large tick marks indicate the beginning of each month, and small tick marks represent 10-d intervals in model simulations beginning January 1, 2001.

the initial fry abundance of 52.4 million and a hydroacoustic estimate of 4.3 million age-1 presmolts in late March 2002; M. Scheuerell, University of Washington School of Aquatic and Fisheries Sciences, unpublished data). The corresponding instantaneous mortality rate was $Z = 3.2189/\text{year}$, or $z = 0.0088/\text{d}$. To estimate daily abundance of fry at large in the lake (N_t), the cumulative abundance of fry remaining from the preceding day (N_{t-1}) was reduced by the daily instantaneous mortality rate ($z = 0.0088$) and then added to the new migrants m_t entering on day t , that is,

$$N_t = m_t + N_{t-1} \cdot e^{-z}.$$

The survival estimate of 4% for the Lake Washington population was considerably lower than the average 32% annual survival rate (range, 2–72%; Table 4 in McGurk 1999) for age 0–1 sockeye salmon or kokanee (lacustrine sockeye salmon) in other lakes. When a weight-dependent estimator

of natural mortality for sockeye salmon and kokanee (McGurk 1999) was applied to age-0–1 sockeye salmon in Lake Washington (based on the geometric mean weight of 0.17 g for age 0 and 10.4 g for age 1 in March), the resulting annual survival estimate was 27%. Because age-0–1 survival rates could vary considerably among years, additional survival scenarios (annual survival of 100, 27, 10, and 4%) were included to assess the effect on abundance of fry during early lake residence. Under these survival scenarios, fry abundance in the lake closely tracked abundance under the no-mortality scenario through early March, then diverged during the latter half of the emigration period (Figure 2). Under the 4% survival scenario, abundance declined from 84% of the no-mortality scenario in mid-March and declined to 59% by the end of the simulation on May 8, whereas abundance under the 27% survival scenario ranged from 93% of the no-mortality option in mid-March to 81% by May 8.

Fry distribution in the lake.—For distribution, size, and diet analysis, sockeye salmon fry were collected in area 5 in southern Lake Washington at night. We used beach seines at nine nearshore sites (February 26–27, March 19–20, April 19, 2001) and, to sample offshore areas, a two-boat surface trawl (March 22 and April 12, 2001) and a Kvichak midwater trawl (March 29, 2001). We also sampled area 2 via the Kvichak midwater trawl (May 5, 2001). The beach seine was 36.6 m long and 2.4 m high at the bag, had 6-mm mesh in the bag, and had 32-m tow lines. The two-boat surface trawl was 15.0 m long, had a cross-section 6.1 m wide \times 3.1 m high, and had mesh that graded from 76.0 mm to 6.4 mm in the cod end; the net was towed at approximately 1 m/s. The Kvichak midwater trawl had a 2.6-m \times 2.6-m cross-section and mesh declining from 76.0 mm to 3-mm knotless mesh in the cod end. Fish sampling commenced at least 1 h after sunset for all sampling methods. Fry were counted and frozen in the field for subsequent growth and diet analyses.

During peak fry immigration, temporal changes in their horizontal and vertical distribution in the lake were determined from a combination of midwater trawling and hydroacoustic surveys. Because of limited funds in 2001, the Kvichak midwater trawl could only be deployed in area 5 during March 29, 2001, but was used extensively in areas 1–5 during March 24–28, 2003. In each area, two to six replicate midwater trawls were towed for 5–10 min at headrope depths of 8 m, 14 m, 21 m, and 30 m. Nocturnal hydroacoustic surveys were

conducted during February 11–12, March 21–22, and April 18–19, 2002, and March 25–26, 2003. During each month, four to five hydroacoustic zig-zag transects were conducted between the eastern and western shores of the lake between the mouth of the Cedar River and the southern tip of Mercer Island; additional offshore transects were taken to survey the longitudinal axis of the lake basin in the east channel (between Mercer Island and the eastern shore) and through the main basins in areas 1–5. The surveys were conducted with a BioSonics DE 6000 sounder and 430-kHz split-beam transducer (6.8° full-beam angle). The species composition of the acoustic targets was inferred from the depth-specific catch composition in the Kvichak midwater trawl and depth-specific target-strength distributions. Identities of surface-oriented acoustic targets were inferred from the catch composition in two-boat surface trawls during March and April 2001.

Diet analysis.—Fish from beach seine, surface trawl, and midwater trawl samples in 2001 (Table 1) were thawed in the laboratory, measured (fork length [FL]; mm), and weighed (nearest 0.01 g). Stomachs were dissected and prey were removed, sorted by species, and counted. Because the stomach contents were often too small to record accurate weights, each prey category was spread to a relatively constant thickness on a Petri dish over a standard grid (0.3-mm squares), and the number of covered grid squares was counted. A grid square was included in the grid count when prey covered more than 50% of the square. The grid counts were used as a surrogate measure of prey weight. For a subsample of stomach contents where the bolus was large enough to weigh directly, a regression of the grid count (GC) versus blotted wet weights (W [mg]) indicated that this method provided an accurate substitute for actual weights of the prey encountered in this study ($r^2 = 0.89$; $N = 12$; $P < 0.00001$):

$$W = -0.085 + 0.022 \cdot GC.$$

Diet data were analyzed by computing the mean proportional contribution of each prey category by grid counts for each sampling date and capture method (beach seining, surface trawling, or midwater trawling; Table 1).

The size distribution of major prey in the diet was measured for each sampling period from a subsample of stomachs with relatively intact prey. Prey were measured to the nearest 0.1 mm from video images taken through a dissecting scope

TABLE 1.—Mean body size and diet composition (proportion by weight) of age-0 sockeye salmon fry by habitat zone and date during 2001. Littoral samples were collected with beach seines (BS), offshore surface samples with surface trawls (ST), and water column samples with midwater trawls (MWT) in southern Lake Washington; *N* = number of net tows.

Gear	Date	Fork length (mm)		Weight (g)		<i>Daphnia</i>	<i>Bosmina</i>	<i>Cyclops</i>	Calanoids	Chironomid pupae	Other	<i>N</i>
		Mean	SD	Mean	SD							
BS	Feb 26–27	29.0	1.6	0.17	0.04	0.16	0.02	0.33	0.09	0.38	0.02	66
BS	Mar 19–20	28.5	3.0	0.17	0.05	0.05	0.00	0.69	0.10	0.15	0.01	60
BS	Apr 19	32.3	6.8	0.33	0.23	0.00	0.00	0.44	0.02	0.52	0.02	18
ST	Mar 22–23	29.0	2.4	0.17	0.07	0.00	0.00	0.72	0.08	0.19	0.00	63
ST	Apr 12	30.8	3.9	0.24	0.13	0.01	0.01	0.89	0.04	0.06	0.00	85
MWT	Mar 26–29	31.9	3.0	0.19	0.12	0.01	0.00	0.96	0.02	0.01	0.00	92
MWT	May 8	37.8	3.8			0.14	0.07	0.71	0.08	0.00	0.00	11

with ImagePro Plus software. The size and counts of major prey were compared with the sizes and densities of prey measured in zooplankton samples from the corresponding periods.

Bioenergetics Modeling

Consumption rates by sockeye salmon fry were estimated from simulations using version 3.0 of the Wisconsin bioenergetics model (Hanson et al. 1997). Consumption rates were compared with the biomass of exploitable prey available in the southern region of Lake Washington during 1 January to 8 May 2001 (simulation days 1–128). The bioenergetics model is an energy balance equation that estimates how much food must be consumed to achieve the observed growth rate while satisfying metabolic demands and waste losses for a consumer over specific time intervals. The model accounts for the effects of daily changes in body size, temperature, prey composition, and energy density on the rates of maximum consumption, metabolism, and waste. Physiological parameters for the sockeye salmon model were taken from Beauchamp et al. (1989); in previous applications of this model, consumption estimates have been within $\pm 10\%$ of independently derived estimates of consumption from two different populations of juvenile sockeye salmon (Beauchamp et al. 1989).

Data inputs for the bioenergetics model were collected during winter–spring 2001 and included growth, habitat-specific diet composition, and thermal experience of fry. Based on the distribution, size, and diet patterns observed from near-shore and offshore samples of fry (Table 1), we constructed a nominal simulation run that reflected the most likely consumption scenario for the majority of fry entering the lake; for comparison, we also developed alternative habitat use scenarios (Table 2).

We assumed that, upon entering the lake, most fry were initially surface-oriented in either near-shore or offshore waters but adopted a midwater distribution pattern within days or weeks after lake entry and were dispersed through at least the southern half of the lake (areas 3–5) by March 2001. Although summarized in more detail in the Results section, our assumptions were based on the following observations: (1) the largest near-shore aggregations of fry only occurred near the Cedar River during February and March, and the size of these fry was nearly identical to the size of downstream migrants; (2) these nearshore aggregations did not reflect the accumulation of fry that would be expected if they remained in near-shore regions for prolonged periods; (3) hydroacoustic surveys in 2002 and 2003 indicated high densities of targets the size of sockeye salmon fry in midwater habitat of area 5 during February, and comparable densities of these targets were dispersed through areas 3–5 by March; (4) midwater trawl catches of sockeye salmon fry were relatively similar among areas 2–5 in March 2003.

Fry size and growth.—We constructed growth cohorts for the bioenergetics model running from January 1 to May 8, 2001. The growth patterns for the nominal and offshore scenarios were inferred from the change in size distributions of fry within and among habitats through time (Figure 3). Growth scenarios were potentially complicated because fry continually entered the lake from January through May at a consistent mean body mass of 0.17 g, whereas fry already in the lake either maintained mass or grew. However, because our objective was to estimate population-level consumption rather than the individual performance of fry, we simplified the growth patterns to reflect the modal body mass of the population. From Feb-

TABLE 2.—Growth and diet inputs used in bioenergetics simulations of age-0 sockeye salmon fry migrating into and feeding in Lake Washington from January 1 to May 8, 2001 (simulation days 1–128). Associated prey energy densities are listed below each prey category.

Simulation day	Weight (g)	Prey				
		Cladocerans (3,800 J/g) ^a	Cyclops (2,260 J/g) ^a	Calanoids (2,260 J/g) ^a	Chironomids (3,400 J/g) ^b	Other (2,930 J/g) ^c
Nominal run						
1	0.17	0.10	0.59	0.06	0.24	0.01
57	0.17	0.09	0.59	0.07	0.24	0.01
81	0.19	0.01	0.84	0.05	0.10	0.00
105	0.24	0.02	0.88	0.04	0.06	0.00
128	0.51	0.21	0.71	0.08	0.00	0.00
Offshore distribution scenario						
1	0.17	0.01	0.84	0.05	0.10	0.00
57	0.17	0.01	0.84	0.05	0.10	0.00
81	0.19	0.01	0.84	0.05	0.10	0.00
105	0.24	0.02	0.88	0.04	0.06	0.00
128	0.51	0.21	0.71	0.08	0.00	0.00
Nearshore distribution scenario						
1	0.17	0.18	0.33	0.09	0.38	0.02
57	0.17	0.18	0.33	0.09	0.38	0.02
81	0.17	0.05	0.69	0.10	0.15	0.01
105	0.33	0.00	0.44	0.02	0.52	0.02
128	0.51	0.00	0.44	0.02	0.52	0.02
Combined offshore–nearshore distribution scenario						
1	0.17	0.10	0.59	0.06	0.24	0.01
57	0.17	0.09	0.59	0.07	0.24	0.01
81	0.18	0.03	0.76	0.07	0.13	0.01
105	0.29	0.01	0.66	0.03	0.29	0.01
128	0.51	0.11	0.57	0.05	0.26	0.01

^a Luecke and Brandt (1993).

^b Values for chironomid pupae were averaged for larval (Hanson et al. 1997) and adult aquatic dipterans (A. Gray, University of Washington, School of Aquatic and Fisheries Sciences, unpublished data).

^c Average of other prey categories.

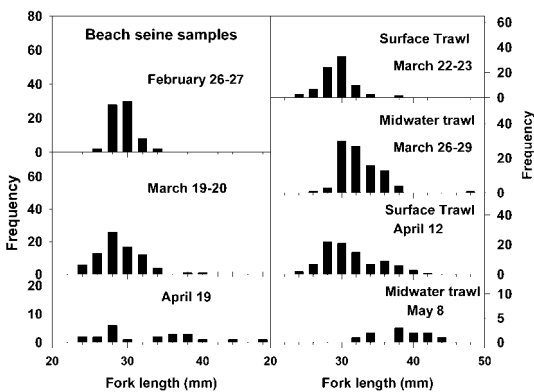


FIGURE 3.—Length frequencies of sockeye salmon fry captured in Lake Washington on different dates during 2001 in nearshore areas with beach seines (left panels) and offshore with two-boat surface trawls or Kvichak midwater trawls (right panels).

ruary through late March 2001, the mean sizes of sockeye salmon fry sampled nearshore in beach seines and offshore in surface trawls were very similar (Table 1), exhibited minimal variability, and were consistent with the size of fry leaving the Cedar River (analysis of variance [ANOVA], $P > 0.20$). Only 20% of the migrants had entered the lake by the end of February, whereas 70% of the fry entered during March. Fry captured in midwater trawls during late March (0.19 g) were significantly larger than fry from nearshore and surface samples during February and March (ANOVA, Dunnett's procedure, $P < 0.001$; Figure 3). Fry from midwater trawls in late March (32 mm FL) and surface trawls on 12 April (31 mm FL) were significantly smaller than fry on May 8, 2001 (38 mm FL; ANOVA, Dunnett's procedure, $P < 0.001$). Therefore, for the nominal and offshore simulations, we specified that fry entering from January 1 through February 26 (simulation day 57) maintained a mass of 0.17 g; then, all fry were

allowed to grow through the rest of the simulation (Table 2). Pilot bioenergetics simulations indicated that holding body mass constant in the simulations through February reduced consumption for the earliest migrants by up to 14% during January and February and increased consumption by 28% in March, resulting in a net 2% reduction over January–March for the earliest 20% of fry entering the lake. However, this effect was overwhelmed by more accurately allowing the 70% of the total fry run that entered in March to grow from 0.17 g at entry to 0.19 g at the end of March and to 0.51 g by May 8, as measured in midwater samples. For fry that might have continued rearing in nearshore waters, body mass was held constant at 0.17 g through late March (day 81), then increased to 0.33 g by mid-April (day 105), based on beach seine samples. Because no nearshore data were available after mid-April, fry in the nearshore scenario were allowed to grow to 0.51 g by May 8, as in the nominal and offshore simulations; body masses from the nearshore and offshore simulations were averaged for the combined nearshore–offshore habitat scenarios (Table 2).

Diet composition and thermal experience.—For the nominal simulation we assumed that fry initially experienced the diet composition (Table 1) and temperatures observed from nearshore samples (January 1 to February 26; simulation days 1–57). These diet proportions and temperature inputs were adjusted daily (via linear interpolation from day 57) to the diet and thermal experience estimated for offshore surface and midwater samples by March 22 (day 81). Because over 70% of the fry population had entered the lake by mid-March and most were dispersed offshore, the model inputs for simulation days 81–128 (March 22 to May 8) were based on offshore growth and diet (Table 2) and thermal experience (Table 3). Temperatures were recorded at 1-m intervals with a Hydrolab for six sampling dates during the study. Nearshore thermal experience was computed as the average temperature (°C) of the 1–5-m depths. Thermal experience for offshore regions used a weighted average based on depth-specific trawl catches and the corresponding depth-specific temperatures.

Alternative habitat use scenarios.—To bracket the potential range of early life history patterns of sockeye salmon fry in the lake, inputs for nearshore, offshore, and combined nearshore–offshore habitat scenarios were included for comparison with the nominal simulation. These scenarios differed in terms of temporal growth and diet com-

TABLE 3.—Thermal experience (varied average temperatures; °C) of age-0 sockeye salmon fry for nominal simulations and habitat-specific scenarios for nearshore, offshore, and combined nearshore–offshore distribution patterns in Lake Washington. Simulation days 1–128 represent January 1 to May 8, 2001.

Simulation day	Nominal run	Distribution scenarios		
		Nearshore	Offshore	Combined
1	8.1	8.1	8.1	8.1
58	7.3	7.4	7.2	7.3
79	7.1	7.5	7.1	7.3
88	7.4	7.7	7.4	7.6
109	8.2	9.7	8.2	9.0
128	9.2	11.1	9.2	10.2

position (Table 2) and thermal experience (Table 3) of fry in three ways. (1) nearshore growth cohorts followed the size distribution and diet patterns observed for winter–spring beach seine data and nearshore temperatures; (2) offshore growth cohorts followed the size distribution and diet patterns observed from surface and midwater trawl samples and offshore temperatures; and (3) a combined growth cohort used the average of the nearshore and offshore growth and diet patterns and the average of the nearshore and offshore temperature values.

Comparing monthly population-level consumption to prey biomass.—The daily cumulative abundance of fry in the lake was multiplied by the corresponding individual daily consumption rate to compute population consumption rates that could be expressed daily, monthly, or seasonally. We assumed that the observed annual survival rate of 4% represented the most realistic abundance trajectory for fry during winter–spring 2001.

Monthly and seasonal consumption rates were compared with the corresponding biomass of exploitable prey available in the southern region of the lake during winter and spring. Monthly population consumption rates of *Cyclops* and total prey were compared with the average monthly biomass of *Cyclops* available to foraging fry in the nominal simulation. Because *Cyclops* was the predominant prey taxon in both the diet and the lake during winter–spring 2001, we reported the consumption; biomass ratios as C/B , where C is total monthly consumption of all prey combined and B is the mean monthly biomass of *Cyclops* available in the depth and area cells specified by the foraging scenario. This ratio reflected the proportional demand on supply as if *Cyclops* were the only available prey. The minimum size of *Cyclops* consumed

by fry (0.8 mm) was used to estimate the fraction of the *Cyclops* biomass consisting of individuals large enough to be eaten. Because production rates for *Cyclops* were extremely low during winter, we used the average of the biomass estimates of exploitable zooplankton for each month as a more conservative measure of food supply. For comparison, a temperature-dependent estimator of daily production: biomass (P/B) for cyclopoid copepods (Shuter and Ing 1997) yielded a P/B of 3.3% to 3.6% per day for our simulations. This degree of production would more than double the prey biomass each month; however, the authors strongly cautioned that these P/B estimators could only legitimately be applied during the growing season.

Sensitivity of Food Demand versus Supply to Fry Dispersal and Survival

We also examined the effects of different fry mortality rates and temporal fry dispersal patterns on made and spatial-temporal comparisons of consumption demand versus biomass of available prey (C/B). Population consumption was simulated using annual fry survival rates ranging from 4% to 100% to determine whether higher survival rates resulted in ecologically significant increases in consumption demand. We used survival rates of 100% (no mortality), 27% (weight-dependent age-0 to age-1 survival prediction for sockeye salmon in Lake Washington; McGurk 1999), 10% (an arbitrary, intermediate rate), and 4% (the survival rate estimated for this year-class of fry). Consumption rates associated with each survival scenario were compared over the full simulation period and during March, when consumption removed the largest fraction of the available prey biomass.

Limited dispersal of fry across various depths and areas of the lake would reduce the biomass of exploitable prey available for consumption. To examine the sensitivity of $C:B$ ratios to horizontal and vertical dispersal by fry, monthly population consumption by fry was concentrated into increasingly restrictive depth and area cells, and access to prey was restricted to just the biomass available within that cell. Because *Cyclops* was the predominant prey in most scenarios, we compared the consumption demand of fry to the biomass of *Cyclops* in area 5, areas 4–5, and areas 3–5, and within depth intervals of 0–10 m, 0–20 m, and 0–30 m.

Effect of Fry Abundance on Growth

We explored the potential for intracohort, density-dependent growth on sockeye salmon fry and

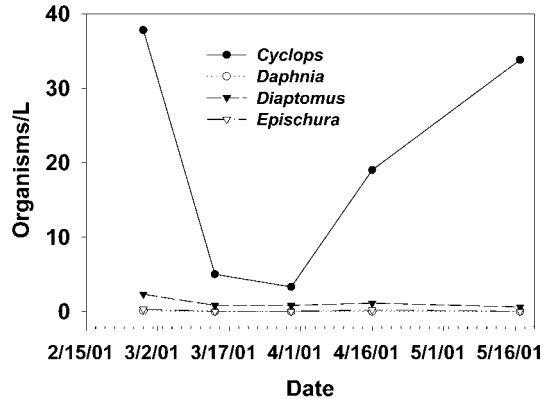


FIGURE 4.—Density of major crustacean zooplankton prey in 0–20-m depths during winter 2001 at station SSE in southern Lake Washington, as sampled with a Clark-Bumpus sampler.

on age-1 presmolts the following year, using 1993–2003 data where such data were available for both the annual abundance of fry migrating from the Cedar River and fork lengths of fry or presmolts. Abundance estimates spanned 5.9 to 52.4 million fry over this period. The fork length of fry or presmolts was regressed against the total abundance of fry entering Lake Washington from the Cedar River. Fry lengths were measured from mid-water trawl samples collected during mid to late April, soon after peak fry immigration (March) and the period of lowest zooplankton density (mid-March through early April). A similar regression was constructed for the fork length of presmolts collected the following year during the last week of March.

Results

Zooplankton Density

Densities of *Cyclops* in the southern region (area 5) of the Lake Washington were more than 30/L in late February but declined precipitously to 2–4/L during March 14–30 before rebounding to 23/L by mid-April and 34/L in mid-May (Figure 4). Meanwhile, densities of *Daphnia* ($<0.1/L$), *Diaptomus* ($\leq 2.4/L$), and *Epischura* ($\leq 0.4/L$) all remained low and relatively constant. *Cyclops* densities also declined considerably from February to mid-March in the central region (area 3), whereas densities increased in the northern region (area 1; Figure 5).

Distribution and Diet of Sockeye Salmon Fry

Nearshore-offshore fry distribution.—Newly entering sockeye salmon fry were initially distrib-

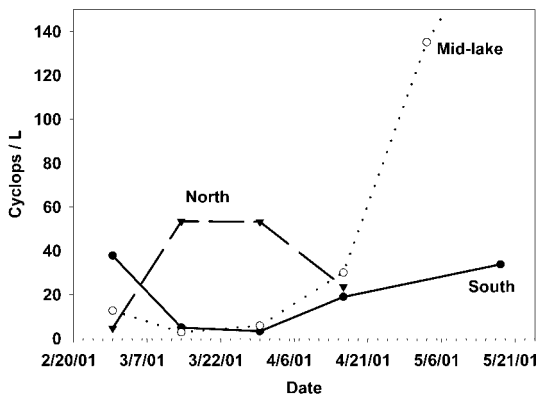


FIGURE 5.—*Cyclops* densities from the 0–10-m depths in daylight tows at the southern (SSE), midlake (MP), and northern (AHP) stations in Lake Washington, as sampled with a Clark-Bumpus sampler during 2001.

uted near the surface in offshore or littoral waters but concentrated in deeper waters and occupied more of the water column as they grew. Through late March, the largest littoral catches of fry were consistently located closest to the mouth of the Cedar River (sites 2–4) and at Mercer Island (site

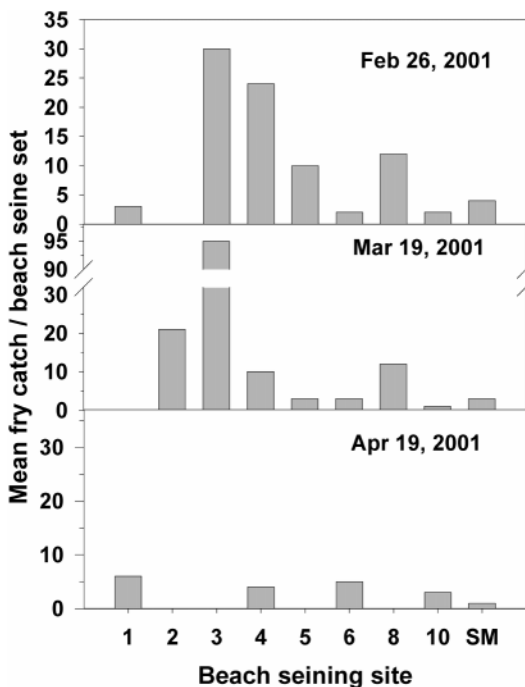


FIGURE 6.—Mean catch of sockeye salmon fry by beach seine site in February, March, and April 2001 in Lake Washington. Sites 2–4 are closest to the Cedar River mouth (see Figure 1).

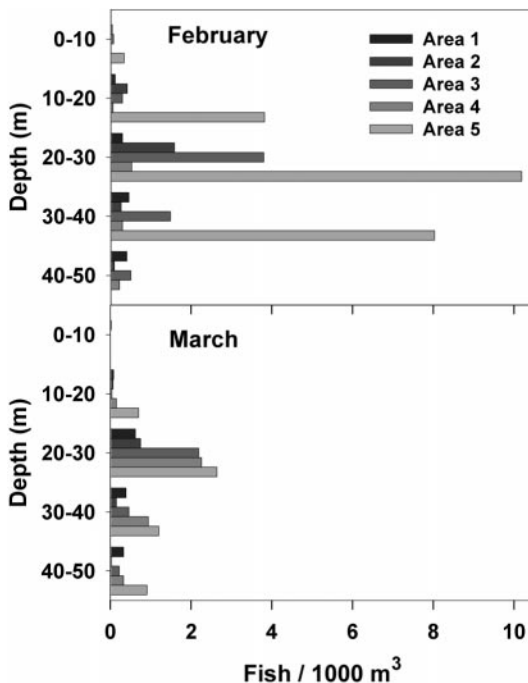


FIGURE 7.—Depth-specific densities of 30–70-mm fish targets in nocturnal hydroacoustic surveys of five areas from Lake Washington, during February and March 2002. Sockeye salmon fry represented 6–66% of the targets in 15–31-m depths, based on depth-specific target-strength data and species composition from Kvichak midwater trawls in area 5 on March 29, 2001 (Table 4) and areas 1–5 during March 24–28, 2003 (Table 5).

8); by April 19, beach seine catches were considerably lower at all sites (Figure 6).

Hydroacoustic and midwater trawl surveys during winter–spring in 2001–2003 indicated that fry dispersed from the Cedar River throughout at least areas 3–5 during February–March and used depths of at least 0–30 m. Dense aggregations of small targets consistent with the size of sockeye salmon fry or yearling longfin smelt (–58 to –52 dB; 30–70 mm TL) were especially evident below 20 m in areas 3–5 (Figure 7). These targets were subsequently verified as sockeye salmon fry and yearling longfin smelt by Kvichak midwater trawl samples in area 5 during March 2001 (Table 4). During March 24–28, 2003, catches of sockeye salmon fry were variable among depths and were relatively high in all areas but were consistently highest at depths of 15 m or more; they represented 2–89% of the catch of all fish captured in these depth × area cells (Table 5).

Temporal diet composition in nearshore and offshore regions.—Cyclopoid copepods were impor-

TABLE 4.—Summary of midwater trawl and surface trawl catches of age-0 sockeye salmon fry and associated species during March–April 2001 in area 5 of Lake Washington. Catches are the averages from 5-min hauls; N = number of net tows.

Depth (m)	Sockeye salmon					N
	Fry	Pre-smolts	Age-0 smelt	Adult smelt	Sticklebacks	
Surface trawl, March 22, 2001						
0–3	23.1	0.0	1.9	0.3	6.5	13
Midwater trawl, March 29, 2001						
8	16.4	0.0	8.8	0.0	3.4	5
14	17.0	0.0	18.6	0.0	20.6	5
21	53.7	0.0	32.8	1.2	19.3	6
30	140.0	4.0	162.5	4.0	17.0	2
Surface trawl, April 12, 2001						
0–3	17.7	0.0	1.0	0.0	24.0	22

tant prey throughout the winter and early spring in both nearshore and offshore habitats, whereas the importance of *Daphnia* and chironomid pupae varied by habitat type and month (Table 1). Fry fed predominantly on *Cyclops* in both nearshore (33–69% of the diet by weight) and offshore zones (71–96%). Loose *Cyclops* eggs were common in the stomach contents, suggesting that many of the *Cyclops* eaten by fry were egg-bearing. *Daphnia* represented 16% of the diet in late February, declined to 0–5% during March–April, then increased to 14% by early May as the spring bloom of *Daphnia* began. Chironomid pupae were important nearshore prey (15–52%) but were less important in near-surface (6–19%) and midwater (0–1%) zones offshore. *Bosmina* (0–7%) and calanoid copepods (2–10%) represented relatively minor fractions of the diet for sockeye salmon fry throughout this early rearing period.

Prey electivity.—Prey electivity could only be calculated for the four available crustacean zooplankton taxa because the availability of chironomids was not measured. Even though *Daphnia* represented a minor fraction of the diet, they were strongly selected by sockeye salmon fry whenever present in nearshore or offshore regions (Chesson's α = 0.55–0.99; Table 6). In contrast, fry exhibited weak positive selection for *Cyclops* offshore during March–April (α = 0.27–0.31) and nearshore during April (α = 0.33). Prey electivity for *Diaptomus* (α = 0–0.07) and *Epischura* (α = 0–0.22) were low and variable in both nearshore and offshore regions.

Size selectivity.—The size distribution of *Cyclops* in the stomachs of sockeye salmon differed

TABLE 5.—Mean catch of age-0 sockeye salmon fry per 5-min haul, by depth and area (upper section of table), and the associated fry percentage of all fish caught during night sampling with a Kvichak midwater trawl, March 24–28, 2003, in Lake Washington.

Depth (m)	Area					East Channel
	1	2	3	4	5	
Mean catch						
7	6.5	7.0	2.5	0.0	12.0	15.0
15	4.0	45.0	3.8	3.5	19.3	175.0
24	8.0	26.5	20.3	25.7	28.0	
28			31.0			
31	2.0	12.0	6.0	20.0		
41		6.0	1.0			
Percentage of fry in the catch						
7	17	17	9	0	46	68
15	14	66	6	5	13	89
24	17	38	19	13	15	
28			40			
31	6	46	7	7		
41		50	2			

significantly from the population in the lake (Kolmogorov–Smirnov two-sample test, $P < 0.001$). The mean total length (TL) of *Cyclops* in the lake during February–March (mean = 0.73 mm, SD = 0.16 mm) was significantly smaller (two-sample t -test, $P < 0.0001$) than *Cyclops* eaten by sockeye salmon fry during that period (mean TL = 1.08 mm, SD = 0.15 mm; Figure 8).

Fry density and feeding in relation to zooplankton densities.—Densities of fry in the littoral zone were generally not correlated with densities of *Cyclops* or total crustacean zooplankton throughout winter–spring in area 5 (r^2 = 0.10, $P > 0.15$), except during late February to early March, when the catch of fry per beach seine haul was positively correlated with *Cyclops* density (r^2 = 0.63, P = 0.03) and total crustacean zooplankton density (r^2 = 0.67, P = 0.02). No relationship existed between the ambient density of zooplankton and either the number or grid counts of prey in stomachs of sockeye salmon fry (r^2 = 0.03, P = 0.50).

Modeling Temporal Consumption and Prey Supply

The nominal simulation assumed that most fry (1) within days or weeks after lake entry shifted from an orientation near the shore or surface to a midwater distribution and foraging pattern, (2) were dispersed through at least the southern half of the lake (areas 3–5) by March, and (3) experienced 4% annual survival from lake entry to late March of the following year. In the nominal sim-

TABLE 6.—Prey electivity (Chesson’s alpha) based on the overlapping of prey fields in time and space with sockeye salmon fry while they were feeding. Positive selection (bold italics) is indicated when values exceed 0.25 (1/N prey types). The unidentified calanoid copepods were composed of *Diaptomus* and *Epischura* that could not be differentiated in stomach samples.

Date	<i>Cyclops</i>	<i>Daphnia</i>	<i>Diaptomus</i>	<i>Epischura</i>	Unidentified calanoids
Beach seine; 0–10-m depths					
Feb 26–27	0.01	<i>0.98</i>	0.00	0.00	0.02
Mar 19–20	0.16	<i>0.78</i>	0.03	0.19	0.06
Apr 19	<i>0.33</i>	<i>0.58</i>	0.01	0.04	0.09
Surface trawl; 0–10-m depths					
Mar 22–23	<i>0.31</i>	<i>0.55</i>	0.07	0.00	nt 0.14
Apr 12	<i>0.27</i>	<i>0.64</i>	0.02	0.22	0.09
Midwater trawl; 0–20-m depths					
Mar 26–29	<i>0.28</i>	<i>0.71</i>	0.00	0.18	0.01
May 8	0.00	<i>0.99</i>	0.00		0.01

ulation, monthly consumption by the fry population in the lake increased from 92 kg of all prey in January (54 kg of this was *Cyclops* and 22 kg was chironomid pupae) to 44,136 kg in April (36,657 kg *Cyclops* and 2,049 kg chironomids; Table 7). Consumption increased rapidly through the season from the combined effects of increasing fry abundance and growth of individual fish.

Consumption rates were relatively insensitive to large changes in fry survival. The effect of different survival rates on consumption was muted in the earlier months but increased through the season. Increasing annual survival from 4% to 100% only increased monthly consumption by 6% in January but increased consumption by 21% in March and 47% in April. Over the full 128-d simulation, a 25-fold increase in survival from 4% to 100% only increased population-level consumption by 46% (Table 7).

In the nominal simulation, monthly population-level consumption on all prey represented 5% or less of the biomass of *Cyclops* available in 0–30-m depths across areas 3–5 (Figure 9). Consumption demand on the available prey biomass (*C/B*) was highest during late March and early April and corresponded with the maximum cumulative abundance of fry in the lake when annual survival rates were 4% or 10%. After early April, *C/B* declined rapidly as zooplankton biomass increased.

Although the nominal simulation indicated that sockeye salmon fry consumed a small fraction of the available food resource, errors in model inputs or interannual variability in habitat use or fry dispersal patterns could change the spatial–temporal dynamics of food supply and demand. In the following section, we examine the sensitivity of these simulations to the major sources of uncertainty or interannual variability (Table 7; Figure 9).

Effect of different habitat use scenarios on monthly consumption rates.—The total biomass of all prey consumed by fry during the 128-d simulation varied minimally (78–82 metric tons) among the nominal, nearshore, offshore, and combined habitat scenarios. Consumption was highest for the

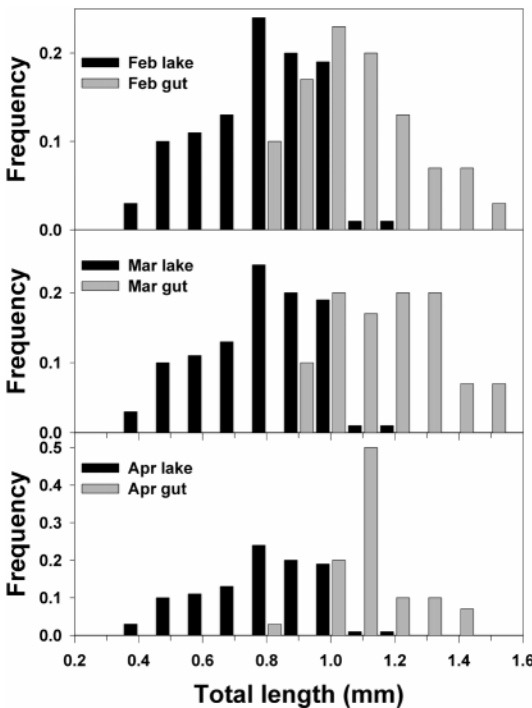


FIGURE 8.—The size distribution of *Cyclops* sampled in the lake and in stomachs of sockeye salmon fry during February–April 2001 in southern Lake Washington.

TABLE 7.—Monthly population-level consumption (kg) by age-0 sockeye salmon fry from January 1 to May 8, 2001, estimated from the nominal bioenergetics model simulation assuming the observed 4% annual survival rate (*S*). The percentage increases in consumption (relative to those at 4% survival) at survival rates of 10, 27, and 100% are also shown.

Month	Consumption by taxon assuming <i>S</i> = 4%						Percent increase in consumption		
	Cladocerans	<i>Cyclops</i>	Calanoids	Chironomids	Other	Total	10%	27%	100%
Nominal growth, diet, and distribution simulation									
Jan	9	54	6	22	1	92	2	3	6
Feb	191	1,278	147	507	21	2,144	3	6	10
Mar	342	10,139	676	1,580	25	12,763	5	11	21
Apr	3,149	36,657	2,281	2,049	0	44,136	11	25	47
May 1–8	4,055	16,390	1,652	198	0	22,295	15	33	64
Total	7,747	64,519	4,761	4,355	47	81,430	11	25	46
Offshore growth, diet, and distribution simulation									
Jan	1	87	5	10	0	103	2	3	6
Feb	24	1,979	118	236	0	2,356	3	6	10
Mar	144	11,075	644	1,262	0	13,124	5	11	20
Apr	3,149	36,657	2,281	2,049	0	44,136	11	25	47
May 1–8	4,055	16,390	1,652	198	0	22,295	15	33	64
Total	7,373	66,187	4,699	3,754	0	82,014	11	25	46
Nearshore growth, diet, and distribution simulation									
Jan	15	28	8	32	2	85	2	3	6
Feb	319	604	162	675	36	1,795	3	6	10
Mar	796	8,743	1,233	3,298	180	14,250	6	13	23
Apr	311	22,239	1,438	22,143	878	47,009	10	23	43
May 1–8	0	6,445	293	7,617	293	14,648	15	33	64
Total	1,441	38,059	3,134	33,766	1,388	77,787	10	23	43
Combined growth, diet, and distribution simulation									
Jan	9	54	6	22	1	92	2	3	6
Feb	183	1,210	140	484	20	2,038	3	6	10
Mar	514	10,265	921	2,372	142	14,214	6	12	22
Apr	1,566	29,748	1,771	12,159	457	45,701	11	24	45
May 1–8	1,678	10,301	830	4,669	177	17,655	15	33	64
Total	3,951	51,578	3,668	19,707	797	79,701	10	23	44

nominal and offshore simulations and included much higher monthly consumption rates on *Cyclops* and other zooplankters, whereas the nearshore and combined scenarios resulted in lower overall consumption and included much greater quantities of chironomids (Table 7). The effects of the different fry survival rates on monthly and overall consumption in all habitat scenarios were very similar to those described for the nominal run (a 25-fold increase in survival resulted in only a 43–47% increase in overall consumption; Table 7).

Sensitivity of food demand versus supply to fry dispersal.—Both zooplankton biomass and population-level consumption by sockeye salmon fry varied considerably among months. In nearly all scenarios, the fraction of the available prey biomass that was consumed by sockeye salmon fry (*C/B*) was very low in January and February, highest in March or April, then declined dramatically in May as zooplankton production increased and

outpaced consumption (Figure 9). Estimates of *C/B* were sensitive to assumptions about the size of the pool of *Cyclops* accessible to foraging fry. Spatial dimensions of this prey pool varied according to assumptions about (1) depth of the water column available to foraging fry (i.e., 0–10 m, 0–20 m, and 0–30 m depth zones), (2) the rate of fry dispersal away from the Cedar River, and (3) the minimum size of zooplankton that could be eaten effectively by fry. Bottlenecks in food supply only emerged under the most restricted dispersal scenarios. If fry were all concentrated in the southernmost region of the lake (area 5) and only had access to *Cyclops* in 0–10-m depths, the monthly consumption by fry would have exceeded the biomass of *Cyclops* during March and April (*C/B* = 98% to 102% at 4% annual fry survival or 123% to 144% at 100% survival); however, *C/B* declined dramatically when foraging scenarios allowed the fry access to prey over a greater range of depths

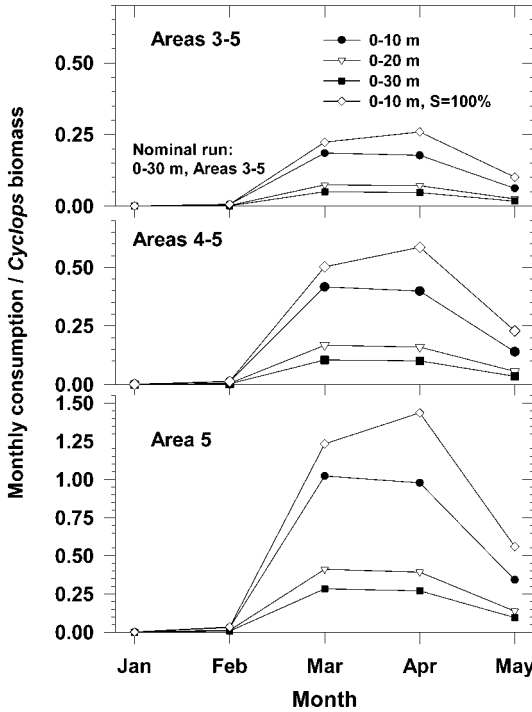


FIGURE 9.—Monthly food demand and supply for sockeye salmon fry assuming an annual survival rate of 4% and different fry dispersal scenarios in Lake Washington. We computed C/B (where C is the total monthly consumption of all prey combined and B is the mean monthly biomass of *Cyclops* available in the depth and area cells specified by the foraging scenario) for the period January 1 to May 8, 2001. In the top panel, fry are assumed to disperse through areas 3–5; in the middle panel, fry are assumed to disperse into areas 4–5; and in the bottom panel, fry are assumed to remain concentrated in area 5. In these scenarios, consumption would exceed the available supply of *Cyclops* if $C/B > 1$. Based on observed fry dispersal patterns in 2002 and 2003, we assumed that fry dispersal throughout areas 3–5 and across depths of 0–30 m (upper panel, solid black squares) represented the most realistic scenario for 2001. For comparison, an additional scenario representing maximum C/B (open diamond) was included, which assumed 100% annual fry survival with fry being restricted to 0–10 m in each area.

and areas (Figure 9). Restricting fry dispersal to fewer areas increased peak monthly C/B more (from 5% for 0–30 m within areas 3–5 to 28% for 0–30 m within just area 5) than restricting the range of accessible depths (5% for 0–30 m to 19% for 0–10 m in areas 3–5). Restricting the accessible depths from 0 to 30 m to 0–20 m had much less effect on C/B than did restricting the depths from 0 to 20 m to 0–10 m (Figure 9).

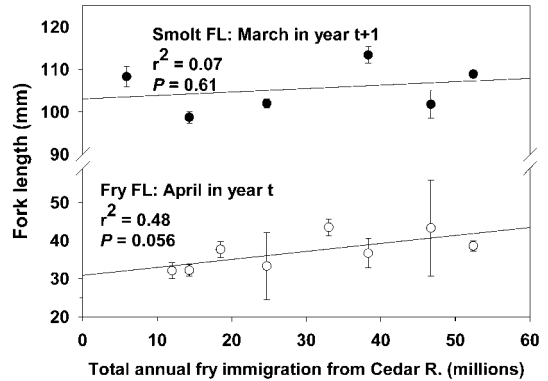


FIGURE 10.—Regressions showing the positive but nonsignificant relationships between sockeye salmon fry abundance (FA) and mean fork length (FL) after peak fry immigration to Lake Washington in mid-April (open circles; $FL = 30.9 + 0.21 \cdot FA$) and mean fork length of the same year-classes as smolts in late March of the following year (filled circles; $FL = 103 + 0.08 \cdot FA$). The results suggest the absence of a density-dependent growth limitation within age-classes of juvenile sockeye salmon. Error bars indicate 2 SEs.

Effect of the minimum edible size of zooplankton on prey supply and demand.—Mean lengths of *Cyclops* in the lake (0.73 mm, SD = 0.16 mm) were smaller than *Cyclops* eaten by sockeye salmon fry (1.08 mm, SD = 0.15 mm). The minimum length of *Cyclops* in stomach samples was 0.8 mm, and 83% of the *Cyclops* biomass was longer than 0.8 mm. If the size distribution of *Cyclops* in stomach samples represented a morphological rather than behavioral size limit for edibility, then estimates of the exploitable biomass of *Cyclops* available each month would be reduced, and C/B would increase accordingly. If we assumed that fry were capable of consuming *Cyclops* longer than 0.8 mm, then consumption would exceed the supply of *Cyclops* longer than 0.8 mm when C/B in Figure 9 exceeded 0.83. This situation only occurred if fry remained concentrated in area 5 and feeding was restricted to *Cyclops* in 0–10 m.

Effect of Fry Abundance on Annual Growth

Density-dependent growth depression was not evident for either the initial short-term growth of fry or for the annual growth of age-1 psmolts (Figure 10). In fact, the fork length of fry exhibited a nearly significant positive correlation with fry abundance after peak immigration ($r^2 = 0.48$, $N = 8$ years, $P = 0.056$) over a range of 12.0 million to 52.4 million fry. Initial fry abundance showed

no correlation with the fork length of presmolts during March in the following year ($r^2 = 0.07$, $N = 6$ years, $P > 0.6$). However, the fork length of presmolts was positively correlated with abundance of the commingled fry from the next year-class ($r^2 = 0.69$, $N = 5$ years, $P = 0.08$).

Discussion

We examined the potential for a temporal-spatial mismatch between consumption demand and food supply during the early lake-rearing phase of sockeye salmon fry. Because our study coincided with the largest recorded migration of 52.4 million fry into the southern end of Lake Washington, these results were particularly relevant for future management of an expanded sockeye salmon fry enhancement program. For comparison, a combined total of 72 million wild and hatchery fry was considered the upper limit to fry production under the new program, which was about 40% higher than the abundance of 52.4 million fry experienced during this study. Because this upper limit depended upon the intersection of abundant naturally spawning adults, high egg incubation survival, and 100% migration survival for hatchery fry, it is highly unlikely that 72 million fry would ever recruit to the lake. Nonetheless, this value provides a useful upper limit for exploring the potential effects of natural and hatchery production on spatial-temporal food demand and supply during winter.

In the nominal simulation, total consumption by 52.4 million fry represented only 5% of the exploitable biomass ($C/B = 5\%$) of the most prevalent prey, *Cyclops*, when food supply was lowest during mid-March through early April. Using the potential maximum abundance of 72 million fry, C/B would increase approximately 40%, from 5% to 7%. To approximate the combined consumption demand by sockeye salmon fry and age-1 presmolts from two consecutive recruitment years with 52.4 million fry, we applied the nominal diet and thermal inputs to the estimated abundance of presmolts that would result from 52.4 million fry (surviving at an annual rate of 4%). The estimated presmolt consumption equated to 1.5 times the monthly consumption rate of fry during peak C/B in March. Therefore, the combined peak consumption demand by fry and presmolts would be 2.5 times C/B for fry during March (5%), and C/B would equal 12.5% when zooplankton biomass was lowest.

Although we lacked sufficient data to describe the spatial-temporal distribution of fry in 2001,

the broad dispersal of fry during 2002 and 2003 (40–45 million fry) suggested that a similar dispersal pattern was likely in 2001, when fry were more abundant (52.4 million). Sensitivity analysis of different fry dispersal scenarios indicated that fry consumption would only exceed prey availability if fry were restricted to 0–10 m depths in area 5. These simulations assumed no new production of zooplankton or replenishment from other depths or areas.

Estimates of consumption and C/B were also insensitive to a broad range of annual survival rates for fry. This was partially a consequence of mortality operating over only 1–128 d instead of a full year, and partially because high immigration rates of fry masked the effects of mortality through mid-March as food supply became most limiting. A possible alternative mortality sequence might begin with extremely high mortality following lake entry (e.g., from an acute predation response) followed by lower mortality during the remainder of the year. This acute mortality scenario would quickly reduce consumption and C/B to even lower levels than the simulations presented here. The nominal simulation assumed that fry initially entered surface waters in offshore or littoral areas (predominantly in the vicinity of the Cedar River) before dispersing over a broader range of depths and areas in the offshore zone. Hydroacoustic and midwater trawling data indicated that sockeye salmon fry dispersed across a relatively broad region of the lake (e.g., areas 3–5) as early as February and throughout the water column by at least March, when prey supplies were lowest. Midwater trawling during March 2001 indicated that fry occupied all depths in area 5, and samples from March 2003 verified that fry were dispersed in substantial numbers across all regions and depths of the lake. From this evidence, we assumed that zooplankton from all depths were either directly available to foraging sockeye salmon fry or were able to replenish any depth-specific depletions within the same area.

In 2001, *Cyclops* were the predominant zooplankton in the lake and in the diet of sockeye salmon fry during the critical immigration and early lake-rearing months of February through mid-May before the *Daphnia* bloom started. *Cyclops* are commonly the primary prey of sockeye salmon fry during the initial lake residence period in other lakes (Burgner 1991; Clarke and Bennett 2002). This was also true in Lake Washington before its recovery from eutrophication and the establishment of *Daphnia* as the predominant zooplankton

(Woodey 1972; Doble and Eggers 1978; Eggers 1978; Edmondson and Litt 1982). Declines in *Cyclops* densities in the southern and central regions of the lake coincided with peak immigration of fry, but densities of *Cyclops* rebounded in April. Chironomid pupae were important in the diets of fry captured in nearshore and near-surface samples but were less important to the majority of fry utilizing the water column offshore, even when zooplankton densities were depressed.

The winter zooplankton community in Lake Washington varies considerably among years, either *Cyclops* (2–50 copepodids/L) or the larger-bodied *Diaptomus* (2–25 adults and copepodids/L) being the predominant crustacean zooplankton (Shepherd et al. 2000). When present, *Diaptomus* were also consumed by sockeye salmon fry (this study) and age-1 presmolts (W. T. Edmondson and A. H. Litt, Department of Zoology, University of Washington, unpublished data). Although juvenile sockeye salmon and other planktivores appear capable of shifting to the prevalent prey species, the interannual variability of crustacean zooplankton abundance and species composition during winter cannot currently be predicted, so real-time monitoring of zooplankton dynamics should be integrated into adaptive management of the sockeye enhancement program.

Although winter fry growth and consumption were well below the maximum rates possible under existing thermal conditions, natural populations rarely feed and grow at maximum rates (Schindler and Eby 1997), especially during winter. Reduced feeding does not necessarily translate into starvation mortality. Clarke and Bennett (2002) reported positive growth (1.5–3.6% average daily increase in dry body mass) and extremely low mortality for newly-emerged, unfed kokanee fry during 21-d growth experiments (preceded by a 4-d starvation period) in net pens in Lake Pend Oreille, Idaho) under prey densities that were similar or lower (0–4.0/L to 0.8–19.1/L) than the lowest densities recorded in southern Lake Washington (0–18 *Cyclops*/L, mean 4.7/L, SD 3.7/L; March 21–22, 2001). The estimated average daily growth rate of 1.5% for fry in Lake Washington from approximately the peak of migration on March 1 to the end of the simulations on May 8 (69 d) was comparable to the 21-d growth rates in Clarke and Bennett's (2002) net pen experiments. As in Lake Washington, the zooplankton community and diet composition of fry in Lake Pend Oreille were both predominated by *Cyclops* during the fry migration period.

Low initial growth rates could increase predation mortality, especially if small, gape-limited predators are abundant (e.g., prickly sculpin [Tabor et al. 1998] and younger age-classes of salmonids and northern pikeminnow). Under these conditions, relatively small increases in body size can translate into significant reductions in the number and type of predators capable of capturing them (Lundvall et al. 1999). Also, ontogenetic shifts in habitat use, behavior, diet, and distribution can also alter predation risk considerably (Werner and Gilliam 1984; Werner and Hall 1988; Walters and Juanes 1993).

Density-dependent growth depression was not evident for either sockeye salmon fry or age-1 presmolts in Lake Washington. Lake Washington produces some of the largest age-1 smolts reported for sockeye salmon populations because of its prolonged growing season and relatively abundant zooplankton (Eggers 1978; Burgner 1991). Rieiman and Myers (1992) reported that density-dependent growth in kokanee populations was not evident for fry but became manifest in age-1 and older kokanee. The sizes of fry and commingled age-1 presmolts from the previous year-class were positively correlated with fry abundance, whereas the size of presmolts showed no correlation to their abundance as recruiting fry the previous spring. This suggests that other factors like interannual variability in zooplankton dynamics, environmental conditions, abundance of competitors, or predator avoidance are more likely to influence growth of juvenile sockeye salmon in Lake Washington rather than the changes in fry abundance that are likely to be experienced under the proposed hatchery operations.

Although our food availability calculations and observations of fry dispersal indicated that fry did not experience a serious food bottleneck in 2001, we caution against assuming that bottlenecks would not occur in future years. Future mismatches in temporal zooplankton supply and feeding demand could still occur, especially in March and early April when prey biomass is lowest. Such mismatches could be created by interannual variation in edible zooplankton density and increased abundance of other planktivores. The combined feeding demand by yearling sockeye salmon, *Neomysis*, threespine sticklebacks, and longfin smelt was estimated to be 3–10 times greater than consumption by sockeye salmon fry during the critical March period (Beauchamp 1996; Beauchamp et al. 2002), but these initial estimates were burdened with considerable uncertainty regarding the diet

composition, abundance, and spatial distribution of these other planktivores during winter. Although consumption by these species might be diversified across more prey species and over more regions of the lake, they could impose significant additional demand on the supply of prey such as *Cyclops* and *Daphnia*. Therefore, an updated analysis of community-level zooplankton supply and demand should be completed to provide a comprehensive assessment of the winter carrying capacity of the lake. Despite uncertainties about communitywide consumption demand, the total consumption by an enhanced sockeye salmon fry population would only account for a small fraction of the available food supply and is unlikely to influence zooplankton dynamics.

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