

**CEDAR RIVER AND LAKE WASHINGTON SOCKEYE SALMON
BIOLOGICAL REFERENCE POINT ESTIMATES**

by

Scott McPherson, MSc., Alaska Department of Fish and Game

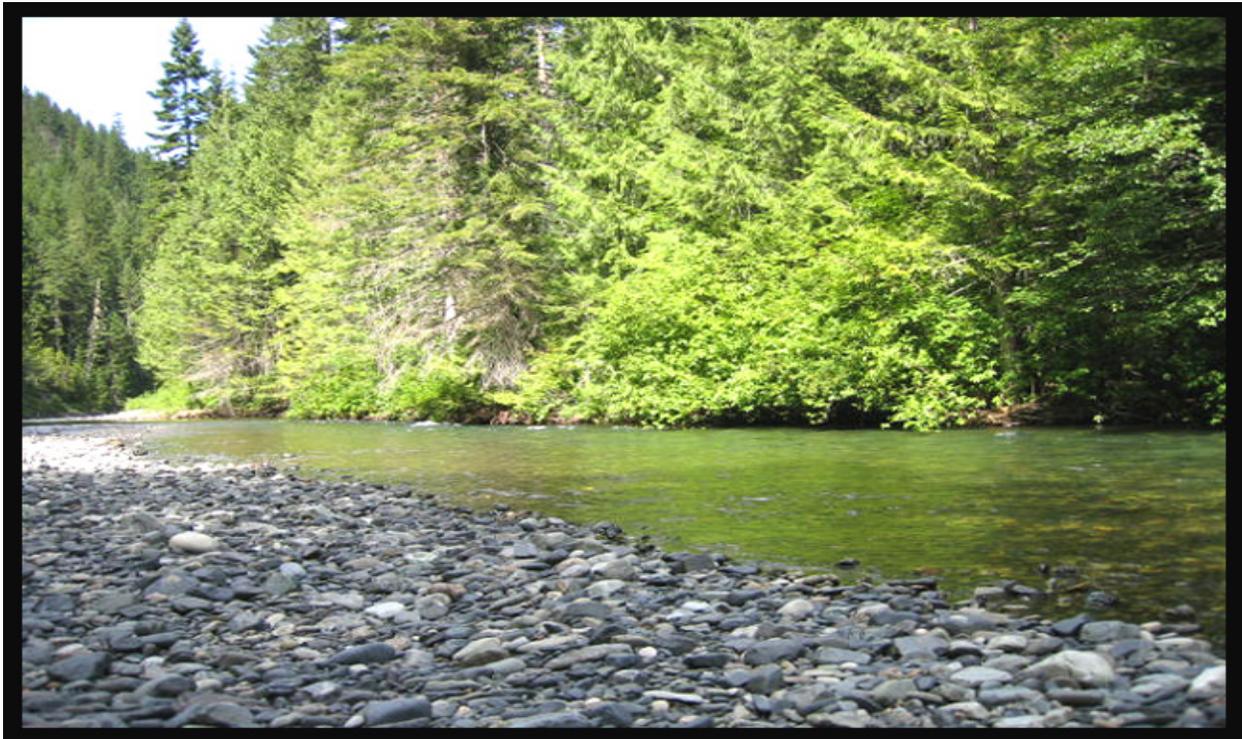
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James C. Woodey, Ph.D., Fisheries Consultant

Submitted to

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Executive summary

1. The objective of the current report is to provide Washington Department of Fisheries and Wildlife with estimates of current Cedar River and Lake Washington natural origin recruit (NOR) sockeye biological reference points (BRPs) to assist in management of the stocks. Analysis of Cedar River and total Lake Washington NOR sockeye abundances in relation to parental spawner population sizes indicated that productivity in the most recent period, 1982-2002, has declined compared to the 1967-1981 period.
2. When data from 1982-2002 were analyzed, our analysis of optimum yield via bias-corrected Ricker stock-recruit (S-R) models produced a relatively low maximum sustained yield (MSY) escapement estimate for Cedar River NOR sockeye of approximately 82,000 spawners. The combined Lake Washington NOR sockeye populations MSY escapement was estimated to be 102,000 natural spawners.
3. Further investigation revealed that even-year brood sockeye recruitment in the 1982-2002 period has been substantially higher than recorded for odd-year broods. Using the Lake Washington spawning escapements to Lock-based recruit dataset, the MSY escapement for even-year broods was relatively stable over the full time period predicting that, on average, 150,000 spawners would generate recruitment of approximately 313,000 fish, yielding 163,000 in surplus production at an optimum harvest rate (HR) of 52%.
4. For the odd-year broods, the 1983-2001 data indicated a MSY escapement of 69,500 spawners compared to 184,000 spawners for the 1967-1981 period. The cause of the decline in odd-year brood productivity in the recent time period could not be determined through S-R analysis.
5. Comparative S-R parameter estimates for eight reference stocks from Washington and southern British Columbia clearly show that current Cedar River productivity is far lower than any of these stocks. The Ricker "a" (alpha) value for the 1982-2002 Cedar River NOR was 1.9 vs. a mean of 8.7 for reference stocks. At MSY, yield from the Cedar River NORs was estimated to be 35,000 from a mean recruitment of 117,000 fish giving an optimum harvest rate of 30% while the mean HR at MSY for the reference stocks was 73%.
6. Analysis of Cedar River NOR sockeye fry recruitment relationships and estimates of fry to presmolt and to adult recruit survival indicates that a bottleneck to production occurs in Lake Washington. Estimated fry to adult survival appears to be quite low and was negatively related to fry abundance. Odd-year brood fry to adult survival was substantially lower than for even-year broods at a given fry

abundance, particularly at higher abundance levels. This pattern of survival was found in hatchery origin (HOR) Cedar River sockeye fry, as well. We estimated through optimization analyses that current yield is highest at approximately 12 million NOR fry for odd-year broods and 21 million fry for even-year broods. The escapements required for these levels of fry recruitment (51,000 Cedar River spawners for odd-year broods and 90,000 for even-year broods) follow the pattern estimated via S-R analysis. Recent levels of NOR fry production have been up to 39 million fry.

7. We hypothesize that foraging by large even-year brood abundances of longfin smelt and other species in late winter exacerbated by large numbers of sockeye fry entering the south end of the lake from the Cedar River prior to the spring bloom period depletes preferred food resources and leads to an extended period of low growth and high mortality that constrains Cedar River NOR sockeye productivity. Interspecific competition between large even-year age 0 smelt populations and juvenile sockeye may be responsible for the lower survival of odd-year brood sockeye fry from the Cedar River. Predation of sockeye fry by large populations of maturing even-year brood longfin smelt or by piscivorous fish after mature even-year broods of smelt spawn and die may account for the differential survival of even- and odd-year brood sockeye.
8. The productivity of the Cedar River sockeye population is very low and would generally limit harvest opportunities at any level of escapement. Yields on future odd-year returns will likely be low under current conditions (MSY yields = 28,000 and 80,500, depending on the assumption for recruitment). Even-year brood recruitment estimates at MSY would likely provide for more regular surplus production and harvest opportunities.

Introduction

The subject of this report is the findings of our inquiry into appropriate biological reference points (BRPs) for Cedar River sockeye and for the Lake Washington sockeye stock complex as a whole. Recent analyses of stream and lake habitat capacity and the recruitment rate for these populations (Ames 2006) provides a rationale for maintenance of an escapement goal policy developed in 1969 which initiates directed fisheries only when the Ballard Lock count-based estimate of return abundance exceeds 350,000 fish. Our goal is to estimate the appropriate BRPs for Cedar River sockeye with data available to us and to provide fishery managers insight into the options and risks of changing the management policy based on current biological measurements. Secondly, we analyze data from other stocks for comparative purposes.

Cedar River sockeye are derived from introductions of eggs and fry from Baker Lake in the 1930s and 1940s and, later, transplantation of Baker Lake stock fry from the Issaquah Creek (Lake Sammamish) hatchery. Escapements increased substantially in the 1960s and programs were initiated to monitor their abundance on spawning grounds in the mid 1960 and at the Hiram M. Chittenden (Ballard) Locks in 1972. Directed commercial fisheries began in 1971 and sport fishing followed shortly thereafter. Subsequent monitoring of spawning populations in other streams and along lake beaches revealed significant populations of spawners, particularly in Bear Creek, a tributary of the Sammamish River, entering the north end of Lake Washington. Genetic studies show that Bear Creek fish are a separate genetic entity (Ames 2006).

Fisheries in marine approach waters and in Lake Washington have yielded catches of up to 376,000 fish in an individual year and account for a total catch of 1,932,000 fish between 1967 and 2006 (mean = 48,300/yr). Escapements to spawning areas in the watershed have ranged from 28,000 to 472,000 fish in the period 1964-2006 (mean = 195,000). Thus, overall, approximately 20% of Lake Washington fish have been harvested. Annual returns of sockeye to the Lake Washington watershed appear to have undergone a shift to lower levels in 1989 to present compared to the estimated returns in the 1967-1988 period (Figure 1). In the following analyses, this apparent shift to lower returns plays a significant role in the treatment of data. We used standard stock-recruit (S-R) analyses, but include analyses of other sockeye stocks to place the productivity of Cedar River sockeye in perspective. We also sought to identify the most likely sources of productivity limitations for Lake Washington sockeye and to determine if future returns would be best characterized by the most recent period data rather than by long-term averages.

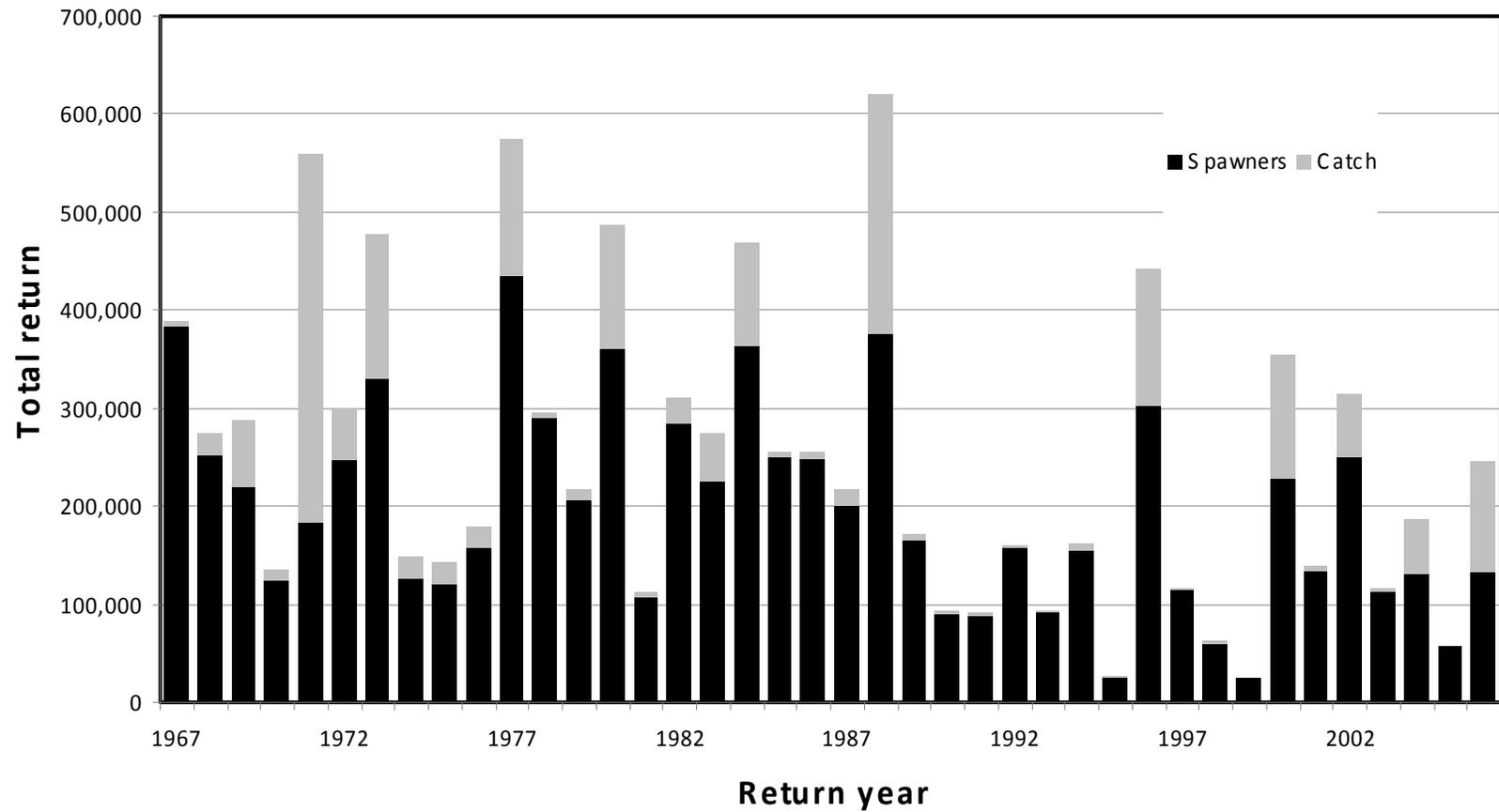


Figure 1—Estimated spawners, catch and total run of Lake Washington sockeye salmon of natural plus hatchery origin for return years 1967-2006.

Background

The location of the Cedar River and Lake Washington in the urban area of Seattle and surrounding communities makes the sockeye population valuable as an indicator of environmental conditions and as a source of revenue and recreation, but also potentially presents limitations and hazards to the resource. Competing demands for Cedar River water as a municipal water source and the need to provide flood control, etc., have resulted in extensive modifications to the primary spawning area. Lake Washington, a naturally mesotrophic lake became eutrophic in the 1950s and 1960s due to the introduction of nutrients associated with the disposal of treated sewage and runoff from farms and residences that rapidly grew to surround the lake in the early to mid 20th Century. Diversion of effluents from the lake in the 1960s resulted in much improved water quality and changes to the lake ecology.

Ames (2006) closely details what is known about the impacts of alterations to the Cedar River and Lake Washington physical and biological stressors to sockeye salmon. Annual introductions of juvenile rainbow trout (*Oncorhynchus mykiss*) for several years began in 1980 and has been suggested as a contributing factor in the decline of average productivity of the stocks beginning in the 1980s. Development of a population of large, predatory cutthroat trout (*O. clarki*) in recent years may be a factor in the continuing low productivity of the Cedar River and other sockeye populations in the watershed. Competitor species in Lake Washington include longfin smelt (*Spirinchus thaleichthys*) and stickleback (*Gasterosteus aculeatus*) and the limnetic (pelagic) mysid shrimp, *Neomysis mercedis*. Smelt and stickleback populations appear to have increased in recent years relative to population sizes in the late 1960s.

In order to mitigate for the removal of water and restriction of access of sockeye in the Cedar River above Landsburg Dam, Seattle Public Utilities instituted a hatchery program for sockeye fry supplementation in 1991. That program has provided approximately 132 million fry over 17 years of operation. Expansion of the fry supplementation program has been proposed and would require taking larger numbers of adult spawners than heretofore and the capacity of the proposed facility would increase the supplementation to a maximum of 34 million sockeye fry.

Studies on juvenile sockeye abundance and growth in Lake Washington began in 1967 (Woodey MS 1972). Subsequent studies provide a rich source of information on the lake and the sockeye and competitor and predator species. Ames (2006) chronicles the introductions of sockeye, population trends and current status of the stocks and provides a valuable list of reference sources for studies to draw from in the future. Beauchamp et al. (2004), Mazur and Beauchamp (2006), Overman et al. (2006) and Overman and Beauchamp (2006 and 2007) provide details of current ecological

conditions and juvenile sockeye and longfin smelt abundance estimates that relate to this study.

Data sources

An extensive dataset exists for analyses focused on the recruitment dynamics of Cedar River/Lake Washington sockeye. These data have been provided to the authors by Washington Department of Fish and Wildlife (WDF&W) and Tribal biologists via WDF&W. Population estimates obtained via area-under-curve (AUC) methods provide the majority of data for Cedar River spawner abundance used in the current study, although methodologies have changed over the years, as has fish distribution in the river.

Recruitment of adult fish to Puget Sound and Lake Washington has been estimated by two different methods. The first method adds spawning escapement estimates plus estimates of catches taken in marine and freshwater areas. The objection to this method has been that en route and prespawning mortalities in the Ship Canal and Lake Washington are not accounted for in the calculation. The second method uses the Lock-based estimates of sockeye entering into freshwater plus marine catch, but finds objections due to the potential “re-cycling” of fish at the Locks wherein fish may enter freshwater, then back out and subsequently, reenter, potentially being estimated two, or more times. These two estimates have been used in sensitivity analyses of S-R parameters. When Lock-based estimates are used, the season totals have been parsed into Cedar River and non-Cedar components. In both datasets, 90% of annual marine and freshwater catches have been attributed to the Cedar River population.

Ballard Lock count-based estimates of annual abundance of returning sockeye to the ship canal and lake in 1972-2008 provide an early indication of the abundance of sockeye for the year. In the 1972-1991 period, Ballard Lock estimates and the cumulative spawning stock estimates plus catch in Lake Washington were in good agreement with spawners plus freshwater catch accounting for a mean of 92% of Ballard Lock estimates (Ames 2006). However, the percentage accounted for in freshwater catch and escapement dropped in the 1992-2004 period to 64%. The disruption of the relationship between Lock estimates and spawners plus catch affects our analyses and the estimation of annual abundance for management of the resource. Herein, we analyze Cedar River/Lake Washington sockeye data using spawning ground estimates of abundance, but also relate Cedar River/Lake Washington sockeye stock-recruit relationships to those obtained by the use of Ballard Lock count-based estimates.

Hatchery fry releases have contributed a portion of the adult Cedar River total returns in 1995-2007. The contribution of hatchery fish is estimated annually through sampling of fish otoliths in the Cedar River for thermal marks on HOR fish. Subtraction of these estimates from the total Cedar River component of the Lake Washington run provides estimates of NOR Cedar River adults that we used in the present analysis. However, those HOR adult sockeye that spawn naturally upon return to Cedar River are considered part of the next generation of NOR fish.

Estimation of Cedar River natural origin and hatchery origin sockeye fry entering Lake Washington began in 1992 with the downstream migration of 1991 brood year fry. The 1991 to 2002 brood year NOR fry estimates (n=12) and corresponding recruitment of NOR adults provide a means of assessing the dynamics of Cedar River sockeye recruitment that were not available previously.

We also examined published data on the abundance of juvenile sockeye in Lake Washington estimated by Overman et al. (2006) and Overman and Beauchamp (2006 and 2007). October and March hydroacoustic and trawl surveys of Lake Washington provided data from which population estimates were derived. We examined these data in light of total natural and hatchery fry estimates from the Cedar River and Bear Creek (Kiyohara and Volkhardt 2007) and from other streams and lake beaches. Fry projections for the latter were obtained for 1998-2007 brood years by applying the annual Bear Creek sockeye fry per spawner estimates to observed abundances of spawners in other streams and beaches. For 1991-1997 broods, an average fry/spawner obtained from Bear Creek sockeye in 1998-2007 was applied to escapements into Bear Creek and other streams. The projections of fry from non-monitored streams and beaches in 1998-2007 were less than 2% of the watershed total, except in 2006 when the projection amounted to 5.7%. All non-Cedar River populations were estimated or projected to have contributed from 0.6 to 27.8% of fry recruiting to Lake Washington (w/o Issaquah Creek – Lake Sammamish sockeye).

Cedar River and Lake Washington sockeye stock-recruitment relationships

We evaluated the stock-recruit relationships for Cedar River sockeye salmon from natural production to estimate parameters from those relationships. We began our examination with the most recent 21 years of Cedar River S-R data, the 1982-2002 brood years, as that was the time period chosen by the co-managers before data analysis began. The quality of data is higher and more complete than for years prior to that time as well. We also examined a longer time series (1967-2002 brood years) to determine if production had been stable over the entire time series available. Data for 1967-1981 brood years were analyzed separately, as well. However, the Cedar River

represents only a portion, albeit the majority, of sockeye salmon production in Lake Washington. Because of this and our need to tie S-R results back to management, we also examined the S-R relationship for all natural production in Lake Washington. To address the issue of unaccounted-for fish after passage through the Ballard Locks, we constructed two S-R data sets incorporating Lock count estimates. All data used in these analyses was provided by WDF&W; several corrections to data noted by Tribal staff members were incorporated before the final draft was completed. In addition, we partitioned the 1982-2002 brood dataset into even- and odd-year broods to delve into observed differences between them in the earlier analyses.

Below, we provide analyses for the following dataset combinations:

1. Cedar River NOR sockeye using estimated spawner abundance for the parent year and spawners plus marine and freshwater catches in the return years to estimate recruits (1982-2002; 1967-2002; and 1967-1981).
2. Lake Washington NOR sockeye using estimated spawner abundance for the parent year and spawners plus marine and freshwater catches in the return years to estimate recruits (1982-2002; 1967-2002; and 1967-1981).
3. Lake Washington NOR sockeye using estimated spawner abundance for the parent year and Ballard Lock-based estimates plus marine catches in return years for recruits (1982-2002; 1967-2002; and 1967-1981).
4. Lake Washington NOR sockeye using Ballard Lock-based estimates less freshwater catch for the parent year and Lock-based estimates plus marine catches in return years for recruits (1982-2002; 1967-2002; and 1967-1981).
5. Lake Washington NOR sockeye using even-year broods (1982-2002; and 1968-1980) and odd-year broods (1983-2001; and 1967-1981) using spawner abundance for the parent year and spawners plus marine and freshwater catches in the return years to estimate recruits
6. Lake Washington NOR sockeye using even-year broods (1982-2002; and 1968-1980) and odd-year broods (1983-2001; and 1967-1981) using spawner abundance for the parent year and Lock-based estimates plus marine catches in the return years to estimate recruits.

Cedar River NOR sockeye

This analysis included estimates of harvest and escapement of sockeye salmon bound for the Cedar River and annual age composition data (Table 1). Harvests for Cedar River fish of natural origin are estimated by assuming that 90% of marine and freshwater harvests are of Cedar River origin, then that estimate is discounted by the

Table 1—Estimated harvest, escapement, annual run size, exploitation rate and age composition of sockeye salmon of natural-origin from the Cedar River, 1967-2007.

Calendar Year	Marine harvest	FW harvest	Total harvest	Escap.	Total run	ER	Age 3	Age 4	Age 5
1967	5,311	0	5,311	365,000	370,311	1.4%			
1968	19,949	0	19,949	240,000	259,949	7.7%			
1969	60,604	0	60,604	200,000	260,604	23.3%			
1970	4,116	5,986	10,102	110,000	120,102	8.4%			
1971	311,785	26,887	338,672	163,363	502,035	67.5%			
1972	13,972	31,443	45,415	225,862	271,277	16.7%	13,265	240,107	17,904
1973	68,840	62,732	131,572	314,194	445,766	29.5%	21,798	406,004	17,964
1974	8,807	12,481	21,289	114,472	135,761	15.7%	6,639	125,837	3,285
1975	16,141	4,542	20,683	114,306	134,989	15.3%	6,874	114,840	13,075
1976	16,795	896	17,690	140,180	157,870	11.2%	16,337	127,614	12,688
1977	82,033	42,272	124,305	421,836	546,141	22.8%	14,587	516,799	2,939
1978	4,794	95	4,890	277,801	282,691	1.7%	2,061	262,190	3,372
1979	7,443	2,236	9,679	185,317	194,996	5.0%	20,291	157,976	3,712
1980	12,107	100,193	112,300	358,489	470,789	23.9%	1,702	438,455	19,970
1981	5,581	69	5,650	94,897	100,547	5.6%	4,191	56,178	35,975
1982	3,144	21,476	24,620	253,658	278,278	8.8%	7,430	267,731	3,117
1983	3,533	41,605	45,139	193,338	238,477	18.9%	3,148	155,320	80,009
1984	4,238	90,005	94,244	336,960	431,204	21.9%	1,811	358,244	71,149
1985	1,921	4,385	6,305	223,745	230,050	2.7%	5,935	173,688	50,427
1986	1,911	5,667	7,578	217,133	224,711	3.4%	2,899	182,578	39,235
1987	1,361	14,153	15,513	177,841	193,354	8.0%	3,693	124,327	65,315
1988	64,842	155,427	220,270	359,000	579,270	38.0%	927	525,282	53,061
1989	3,529	1,605	5,134	162,000	167,134	3.1%	602	59,767	106,765
1990	1,524	2,762	4,286	76,000	80,286	5.3%	1,076	54,434	24,889
1991	2,617	668	3,285	78,259	81,544	4.0%	1,333	63,931	14,772
1992	2,167	221	2,389	101,648	104,037	2.3%	102	64,536	37,720
1993	1,339	215	1,554	80,562	82,116	1.9%	194	64,719	12,610
1994	6,001	281	6,282	112,798	119,080	5.3%	161	105,252	9,845
1995	344	339	684	23,807	24,490	2.8%	838	19,061	1,795
1996	27,618	92,930	120,549	228,593	349,142	34.5%	0	263,157	78,605
1997	1,586	193	1,779	93,721	95,500	1.9%	0	69,819	21,075
1998	2,756	0	2,756	47,040	49,797	5.5%	0	28,718	16,915
1999	598	0	598	16,790	17,388	3.4%	0	3,313	12,989
2000	19,124	71,182	90,306	126,185	216,491	41.7%	115	196,844	12,569
2001	1,694	2,442	4,136	102,633	106,769	3.9%	0	86,251	15,768
2002	5,719	29,006	34,725	120,209	154,935	22.4%	0	129,502	20,132
2003	1,742	365	2,107	70,375	72,482	2.9%	0	58,038	11,419
2004	4,741	30,301	35,042	90,578	125,620	27.9%	0	104,696	14,751
2005	288	0	288	40,940	41,228	0.7%	2,974	28,552	6,543
2006	7,506	63,624	71,130	80,316	151,446	47.0%	122	132,510	13,471
2007	798	0	798	31,301	32,099	2.5%	484	1,029	29,728
Averages									
1967-07	19,779	22,407	42,185	165,150	207,335	14.1%	3,933	160,203	26,543
1967-81	42,552	19,322	61,874	221,714	283,588	17.0%	10,775	244,600	13,088
1982-07	6,640	24,187	30,827	132,516	163,343	12.3%	1,302	127,742	31,718

percent HOR fish in the return to the Cedar River (applicable in 1995 to present). Annual escapements to the Cedar River are the number of fish estimated to spawn in the Cedar River, regardless of origin. In estimating recruitment from NORs, however, the portion of the return estimated to be of hatchery origin is not included.

Estimated production of natural-origin adults from brood year y was calculated as:

$$\hat{R}_y = \sum_{i=3}^5 \hat{N}_{1.i,y+i+2}$$

where $\hat{N}_{1.i,y+i+2}$ is the estimated escapement and harvest of natural salmon age-1. i in year $y+i+2$ (age classes 1.1, 1.2 and 1.3 or total age 3, 4 and 5 fish). Note that some subyearling sockeye in Lake Washington smolt in early summer, which should result in adults of age classes 0.1, 0.2 and 0.3 or total age 2, 3 and 4 fish (E. Warner, fishery biologist, Muckleshoot Tribe, pers. comm.). However, these age classes were not included in the dataset provided to the Panel. Estimated total production by age for Cedar River natural-origin fish are in Table 2 for brood years 1967-2002.

The S-R model used in this analysis was Ricker's exponential function (Ricker 1975):

$$R_y = \alpha S_y \exp(-\beta S_y) \exp(\varepsilon_y),$$

Where R_y is the estimated total return for year class y , S_y is the estimated spawners for year class y and α and β are parameters to be estimated.

Parameters were estimated for the linear form of Ricker's model (Table 3):

$$\ln(R_y) - \ln(S_y) = \ln(\alpha) - \beta S_y + \varepsilon_y.$$

A further explanation of parameters utility is given in the reference stock section below. Predictions by the fitted, untransformed model and the original data for the 1982-2002 brood year are given in Figure 2; and for the 1967-1981 brood years in Figure 3. The original data for the entire data set (1967-2002 broods) appear in Figure 4 and the residuals from all three fits in Figure 5.

Table 2—Estimated parent-year escapements (S) and adult recruits (R) of sockeye salmon of natural origin from the Cedar River for brood years 1967-2002.

Brood Year	Parent-year escapement (S)	Brood year total returns (R)				R/S
		Age 3	Age 4	Age 5	Total (R)	
1967	365,000	5,819	463,941	17,904	487,664	1.3
1968	240,000	18,204	240,107	17,964	276,275	1.2
1969	200,000	13,265	406,004	3,285	422,554	2.1
1970	110,000	21,798	125,837	13,075	160,709	1.5
1971	163,363	6,639	114,840	12,688	134,167	0.8
1972	225,862	6,874	127,614	2,939	137,427	0.6
1973	314,194	16,337	516,799	3,372	536,509	1.7
1974	114,472	14,587	262,190	3,712	280,489	2.5
1975	114,106	2,061	157,976	19,970	180,006	1.6
1976	138,949	20,291	438,455	35,975	494,721	3.6
1977	275,000 ¹	1,702	56,178	3,117	60,997	0.1
1978	262,733	4,191	267,731	80,009	351,931	1.3
1979	172,300	7,430	155,320	71,149	233,898	1.4
1980	347,827	3,148	358,244	50,427	411,819	1.2
1981	90,694	1,811	173,688	39,235	214,734	2.4
1982	253,658	5,935	182,578	65,315	253,828	1.0
1983	193,338	2,899	124,327	53,061	180,287	0.9
1984	336,960	3,693	525,282	106,765	635,740	1.9
1985	223,745	927	59,767	24,889	85,582	0.4
1986	217,133	602	54,434	14,772	69,808	0.3
1987	177,841	1,076	63,931	37,720	102,727	0.6
1988	359,000	1,333	64,536	12,610	78,479	0.2
1989	162,000	102	64,719	9,845	74,667	0.5
1990	76,000	194	105,252	1,795	107,241	1.4
1991	76,685	161	19,061	78,605	97,828	1.3
1992	99,588	838	263,157	21,075	285,071	2.9
1993	74,860	0	69,819	16,915	86,734	1.2
1994	108,050	0	28,718	12,989	41,707	0.4
1995	21,309	0	3,313	12,569	15,882	0.7
1996	228,082	0	196,844	15,768	212,612	0.9
1997	102,581	115	86,251	20,132	106,498	1.0
1998	48,384	0	129,502	11,419	140,921	2.9
1999	21,755	0	58,038	14,751	72,789	3.3
2000	146,061	0	104,696	6,543	111,239	0.8
2001	117,225	0	28,552	13,471	42,023	0.4
2002	192,395	2,974	132,510	29,728	165,212	0.9
Averages						
1967-2002	176,976	4,584	173,061	26,543	204,188	1.3
1967-1981	208,967	9,610	257,662	24,988	292,260	1.6
1982-2002	154,126	993	112,633	27,654	141,280	1.1

¹ The 1977 spawning abundance was discounted from 410,020 to 275,000 spawners based on observed pre-spawning mortality.

Table 3 (Panel A)—Parameter estimates from the log-linear transform of Ricker’s model on estimates of adult production and spawning abundance for Lake Washington and Cedar River sockeye salmon stocks of natural origin, for brood years 1982-2002.

Data	Counted Catch & Escapement	Lock Esc to Lock Recruits	Counted Esc to Lock Recruits	Counted Catch & Escapement
Stock	Lk Washington	Lk Washington	Lk Washington	Cedar R
$\ln(\hat{\alpha})$	0.4660 (P = 0.0395)	0.5554 (P = 0.0696)	0.8119 (P = 0.0107)	0.4063 (P = 0.1864) ¹
$\ln(\hat{\alpha}) + \sigma_{\varepsilon}^2 / 2$	0.6897	0.7341	1.0138	0.6480
$\hat{\alpha}$	1.9931	2.0835	2.7559	1.9117
$\hat{\beta}$	0.00000304 (P=0.0456)	0.00000283 (P=0.0266)	0.00000363 (P=0.0153)	0.00000358 (P=0.0434)
$1/\hat{\beta} = \hat{S}_{MAX}$	329,000	354,000	276,000	280,000
\hat{S}_{EQ}	227,000	260,000	279,000	181,000
R ² (corrected)	0.149	0.193	0.234	0.156
$\hat{\sigma}_{\varepsilon}^2$	0.4600	0.3572	0.4037	0.4833
\hat{S}_{MSY}	102,243	116,440	119,856	82,396
90% CI	66,000 to 163,000	83,000 to 164,000	89,000 to 186,000	49,000 to 133,000
90% MSY range	69,000 to 140,000	78,000 to 159,000	79,000 to 166,000	55,000 to 112,000
MSY	47,000	58,000	94,000	35,000
Contrast \hat{S}	15.9	12.6	15.7	16.8
\hat{U}_{MSY} (ER)	0.35	0.33	0.44	0.30

¹ Flags a non-significant parameter value.

Table 3 (Panel B)—Parameter estimates from the log-linear transform of Ricker’s model on estimates of adult production and spawning abundance for Lake Washington and Cedar River sockeye salmon stocks of natural origin, for brood years 1967-1981.

Data	Counted Catch & Escapement	Lock Esc to Lock Recruits ¹	Counted Esc to Lock Recruits	Counted Catch & Escapement
Stock	Lk Washington	Lk Washington	Lk Washington	Cedar R
$\ln(\hat{\alpha})$	0.9267 (P = 0.0524)	1.1795 (P = 0.0670)	1.0456 (P = 0.0070)	0.8812 (P = 0.0571)
$\ln(\hat{\alpha}) + \sigma_{\epsilon}^2 / 2$	1.1125	1.3048	1.1573	1.0783
$\hat{\alpha}$	3.0418	3.6869	3.1622	2.9379
$\hat{\beta}$	0.00000274 (P=0.1479) ²	0.00000361 (P=0.1271) ²	0.00000279 (P=0.0579)	0.00000289 (P=0.1447) ²
$1/\hat{\beta} = \hat{S}_{MAX}$	365,000	277,000	358,000	345,000
\hat{S}_{EQ}	406,000	362,000	412,000	373,000
R ² (corrected)	0.089	0.174	0.192	0.091
$\hat{\sigma}_{\epsilon}^2$	0.3716	0.2506	0.2113	0.3943
\hat{S}_{MSY}	171,440	147,894	172,961	158,137
90% CI	114,000 to 429,000	107,000 to 302,000	125,000 to 381,000	108,000 to 390,000
90% MSY range	113,000 to 238,000	97,000 to 207,000	110,000 to 246,000	98,000 to 227,000
MSY	155,000	172,000	165,000	136,000
Contrast \hat{S}	3.6	2.7	3.6	4.0
\hat{U}_{MSY} (ER)	0.31	0.53	0.42	0.46

¹ Includes brood years 1972-1981.

² Flags a non-significant parameter value.

Table 3 (Panel C)—Parameter estimates from the log-linear transform of Ricker’s model on estimates of adult production and spawning abundance for Lake Washington, Cedar River and non-Cedar River sockeye salmon stocks of natural origin, for brood years 1967-2002.

Data	Counted Catch & Escapement	Lock Esc to Lock Recruits ¹	Counted Esc to Lock Recruits	Counted Catch & Escapement
Stock	Lk Washington	Lk Washington	Lk Washington	Cedar R
$\ln(\hat{\alpha})$	0.5520 (P = 0.0395)	0.6560 (P = 0.0177)	0.8406 (P = 0.0007)	0.4549 (P = 0.0817) ²
$\ln(\hat{\alpha}) + \sigma_{\epsilon}^2 / 2$	0.7820	0.8259	1.0153	0.7087
$\hat{\alpha}$	2.1859	2.2921	2.7603	2.0313
$\hat{\beta}$	0.00000238 (P=0.0456)	0.00000266 (P=0.0158)	0.00000290 (P=0.0065)	0.00000240 (P=0.0668) ²
$1/\hat{\beta} = \hat{S}_{MAX}$	421,000	375,000	345,000	417,000
\hat{S}_{EQ}	329,000	311,000	350,000	296,000
R ² (corrected)	0.086	0.157	0.175	0.069
$\hat{\sigma}_{\epsilon}^2$	0.4600	0.3469	0.3495	0.5075
\hat{S}_{MSY}	146,508	137,557	150,303	133,145
90% CI				
90% MSY range	98,000 to 201,000	92,000 to 189,000	100,000 to 208,000	89,000 to 182,000
MSY	80,000	81,000	118,000	63,000
Contrast \hat{S}	15.9	26.2	15.9	17.1
\hat{U}_{MSY} (ER)	0.35	0.37	0.44	0.32

¹ Includes brood years 1972-2002.

² Flags a marginally significant parameter value.

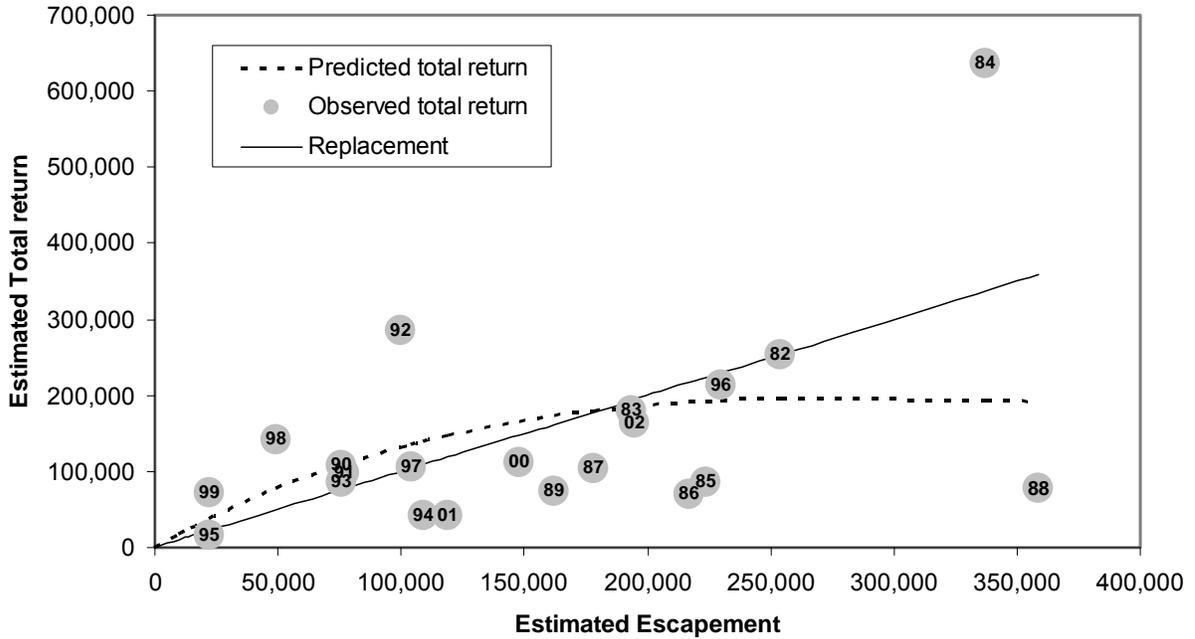


Figure 2—Estimated production of adult sockeye salmon of natural origin from the Cedar River in brood years 1982-2002 against the estimated escapement, along with curves corresponding to least-squares fit of the Ricker model and the replacement line.

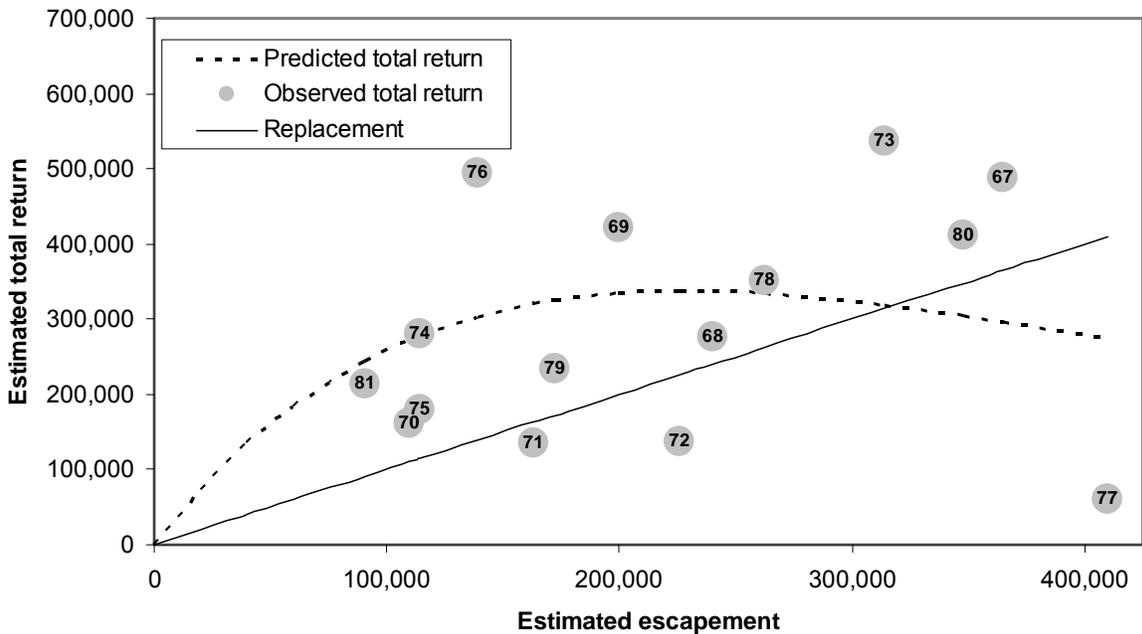


Figure 3—Estimated production of adult sockeye salmon of natural origin from the Cedar River in brood years 1967-1981 against the estimated escapement, along with curves corresponding to least-squares fit of the Ricker model and the replacement line.

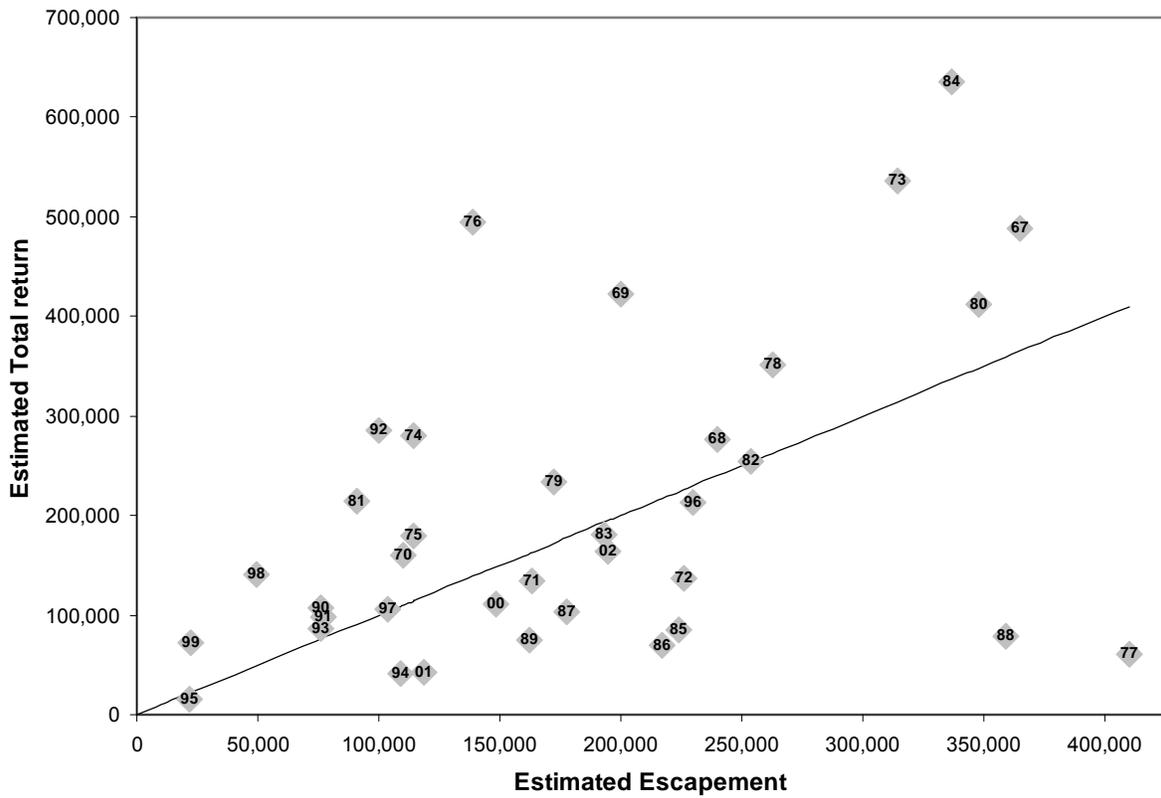


Figure 4—Estimated production of adult sockeye salmon of natural origin from the Cedar River in brood years 1967-2002 against the estimated escapement, along with the replacement line. A model fit line is not shown for this data set due to the change in productivity since 1967.

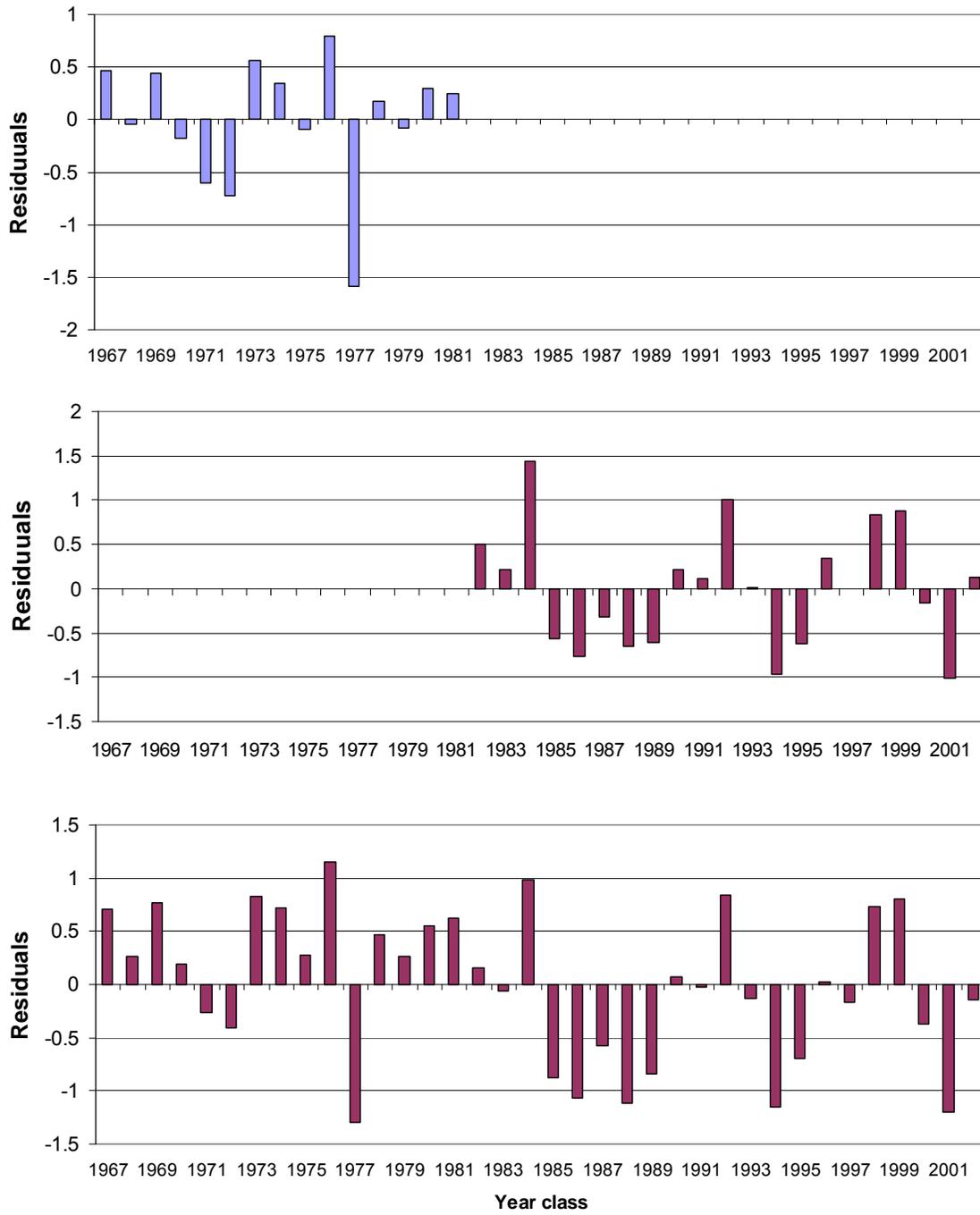


Figure 5—Estimated residuals of the log-transformed fit of the Ricker model to production of adult sockeye salmon of natural origin from the Cedar River for three fits of the 1967-2002 brood years. The top and middle panels are residuals to the fit for those broods only.

No autocorrelation among residuals (Durbin-Watson test = 1.55) was detected for the 1982-2002 broods, nor the 1967-1981 broods when these time series were fit separately, but autocorrelation appeared to be present when all broods (1967-2002) were fit to the Ricker model. For this latter fit the residuals were mostly positive for the 1967-1984 brood years and mostly negative for the 1985-2002 brood years. This indicates a change in the magnitude of production over time, in this case a decrease.

Spawning abundance that on average produces maximum sustained yield (S_{MSY}) can be estimated by iteratively solving the following transcendental relationship:

$$1 = (1 - \hat{\beta}\hat{S}_{msy}) \exp(-\hat{\beta}\hat{S}_{msy}) \exp(\ln \hat{\alpha} + \hat{\sigma}_\varepsilon^2/2)$$

for \hat{S}_{MSY} where $\hat{\sigma}_\varepsilon^2$ is the mean square error from the fitted regression.

When $0 < \ln(\alpha) < 3$, \hat{S}_{MSY} can be approximated without involving iteration. Hilborn and Walters (1992:271-2) published the following empirical approximation:

$$\hat{S}_{MSY} \cong \frac{\ln \hat{\alpha} + \hat{\sigma}_\varepsilon^2/2}{\hat{\beta}} [0.5 - 0.07(\ln \hat{\alpha} + \hat{\sigma}_\varepsilon^2/2)],$$

which we used to estimate \hat{S}_{MSY} . This approximation holds only when spawning abundance and production are measured in the same units and no covariates are included in the analysis.

The stock-recruit data for the 1982-2002 broods resulted in an estimated \hat{S}_{MSY} of 82,000 spawners in the Cedar River (Table 3, Panel A), with a range that would, on average, produce 90% of MSY from 55,000 to 112,000 spawners. The 90% confidence interval around \hat{S}_{MSY} was relatively large however, from 49,000 to 133,000 fish.

Simulations were developed to estimate the probability of achieving MSY from the Cedar River catch and escapement data presented to us, where 1,000 iterations of the original set of spawners were paired with the predicted returns plus an original residual (with replacement). From this, we estimate that there is a 60% probability of attaining > 90% of MSY between spawning escapements of 60,000 and 100,000 spawners in the Cedar River, using the 1982-2002 brood year data (Figure 6). This percentage drops to 20% at escapements of about 140,000 spawners. Note that the probability never climbs above 78% because of the poor fit of the data.

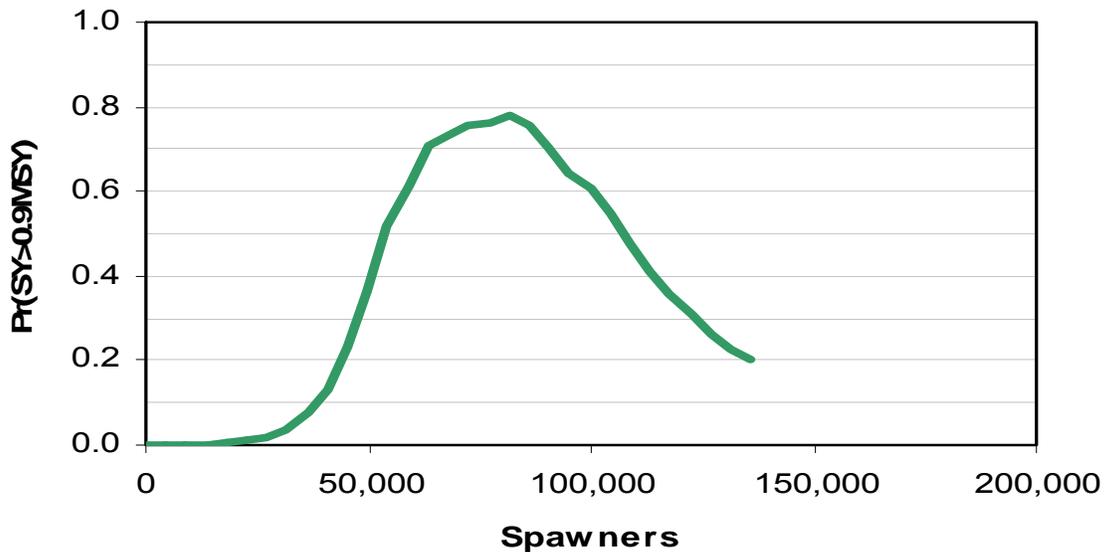


Figure 6—Probability that a specified spawning abundance will result in sustained yield exceeding 90% of maximum sustained yield for Cedar River sockeye salmon, brood years 1982-2002.

The data for the 1967-1981 broods resulted in an estimated \hat{S}_{MSY} of 158,000 spawners in the Cedar River, with a 90% MSY range of 98,000 to 227,000 spawners (Table 3, Panel B). The 1982-2002 data set produces some nonsensical results as discussed further in the reference stocks section below, including a non-significant Ricker a parameter ($P = 0.186$), while the 1967-1981 data set produced more sensible parameters estimates, i.e., S_{MAX} (345,000 fish) was less than replacement ($S_{eq} = 373,000$ fish), etc.

In the earlier, more productive, portion of the time series, the data indicate that the theoretical exploitation rate that could be applied at \hat{S}_{MSY} was 46%, compared to 30% for the 1982-2002 broods. Note that the observed exploitation rates for the two time series is 17% and 13% (Table 1).

All Lake Washington NOR sockeye

Because management and harvest occurs on all Lake Washington sockeye salmon stocks, we looked at the aggregate data as well. Estimates of harvest and escapement of all natural-origin sockeye salmon and annual age composition data are in Table 4. These are the sum of all harvest and escapement estimates for Lake Washington and discounted for hatchery production from 1995 to 2007. Estimated total production by age and brood for Lake Washington natural-origin fish are in Table 5 for brood years 1967-2002.

Table 4—Estimated harvest, escapement, annual run size, exploitation rate and age composition of sockeye salmon of natural-origin from all Lake Washington stocks, 1967-2007.

Calendar year	Total harvest	Escap.	Total annual run	ER	Age 3	Age 4	Age 5
1967	5,901	383,250	389,151	1.5%			
1968	22,165	252,000	274,165	8.1%			
1969	67,338	220,000	287,338	23.4%			
1970	11,224	124,000	135,224	8.3%			
1971	376,302	182,201	558,503	67.4%			
1972	50,461	248,448	298,909	16.9%	14,617	264,564	19,728
1973	146,191	329,904	476,095	30.7%	23,281	433,627	19,187
1974	23,654	125,919	149,573	15.8%	7,314	138,639	3,620
1975	22,981	120,011	142,992	16.1%	7,293	121,829	13,870
1976	19,656	160,440	180,096	10.9%	18,784	146,724	14,588
1977	138,117	447,536	585,653	23.6%	15,988	566,444	3,221
1978	5,433	304,651	310,084	1.8%	2,388	303,789	3,907
1979	10,754	218,817	229,571	4.7%	25,597	199,291	4,683
1980	124,778	371,411	496,189	25.1%	1,836	472,818	21,535
1981	6,278	110,805	117,083	5.4%	5,093	68,271	43,719
1982	27,355	289,774	317,129	8.6%	8,467	305,110	3,552
1983	50,154	229,671	279,825	17.9%	3,694	182,250	93,881
1984	104,715	372,525	477,240	21.9%	2,004	396,491	78,745
1985	7,006	253,135	260,141	2.7%	6,712	196,406	57,023
1986	8,420	251,061	259,481	3.2%	3,347	210,828	45,305
1987	17,237	204,705	221,942	7.8%	4,239	142,731	74,972
1988	244,744	377,806	622,550	39.3%	996	564,528	57,026
1989	5,704	166,972	172,676	3.3%	622	61,749	110,305
1990	4,762	93,825	98,587	4.8%	1,321	66,704	30,562
1991	3,650	89,526	93,176	3.9%	1,547	74,485	17,144
1992	2,654	161,307	163,961	1.6%	164	103,394	60,403
1993	1,727	99,101	100,828	1.7%	252	84,181	16,395
1994	6,980	163,923	170,903	4.1%	239	156,069	14,595
1995	763	28,003	28,765	2.7%	1,105	25,296	2,364
1996	134,475	304,214	438,689	30.7%	0	337,791	100,898
1997	2,009	104,847	106,856	1.9%	0	82,080	24,776
1998	3,111	58,154	61,265	5.1%	0	38,555	22,709
1999	692	19,070	19,761	3.5%	0	4,016	15,746
2000	102,780	208,275	311,056	33.0%	171	292,225	18,660
2001	4,695	117,563	122,258	3.8%	0	103,362	18,896
2002	41,261	176,909	218,170	18.9%	0	188,818	29,352
2003	2,491	73,740	76,231	3.3%	0	63,699	12,532
2004	40,438	106,642	147,080	27.5%	0	128,917	18,163
2005	331	46,764	47,095	0.7%	3,679	35,321	8,094
2006	82,406	107,043	189,449	43.5%	159	171,822	17,468
2007	931	35,850	36,780	2.5%	570	1,212	34,998
Averages							
1967-2007	47,140	188,776	235,915	13.6%	187,057	31,462	4,486
1967-1981	68,749	239,960	308,708	17.3%	271,600	14,806	12,219
1982-2007	34,673	159,246	193,919	11.5%	154,540	37,868	1,511

Table 5—Estimated parent-year escapements (S) and adult recruits (R) of sockeye salmon of natural origin from all Lake Washington stocks for brood years 1967-2002.

Brood year	Parent-year escapement (S)	Brood year total returns (R)			Total (R)	R/S
		Age 3	Age 4	Age 5		
1967	383,250	6,612	527,206	19,728	553,546	1.4
1968	252,000	20,686	264,564	19,187	304,437	1.2
1969	220,000	14,617	433,627	3,620	451,864	2.1
1970	124,000	23,281	138,639	13,870	175,790	1.4
1971	182,201	7,314	121,829	14,588	143,731	0.8
1972	248,448	7,293	146,724	3,221	157,238	0.6
1973	329,904	18,784	566,444	3,907	589,135	1.8
1974	125,919	15,988	303,789	4,683	324,461	2.6
1975	119,811	2,388	199,291	21,535	223,213	1.9
1976	159,209	25,597	472,818	43,719	542,134	3.4
1977	300,700 ¹	1,836	68,271	3,552	73,659	0.2
1978	289,583	5,093	305,110	93,881	404,084	1.4
1979	205,800	8,467	182,250	78,745	269,462	1.3
1980	360,749	3,694	396,491	57,023	457,208	1.3
1981	106,602	2,004	196,406	45,305	243,716	2.3
1982	289,774	6,712	210,828	74,972	292,512	1.0
1983	229,671	3,347	142,731	57,026	203,104	0.9
1984	372,525	4,239	564,528	110,305	679,073	1.8
1985	253,135	996	61,749	30,562	93,307	0.4
1986	251,061	622	66,704	17,144	84,470	0.3
1987	204,705	1,321	74,485	60,403	136,209	0.7
1988	377,806	1,547	103,394	16,395	121,335	0.3
1989	166,972	164	84,181	14,595	98,940	0.6
1990	93,825	252	156,069	2,364	158,686	1.7
1991	87,952	239	25,296	100,898	126,434	1.4
1992	159,247	1,105	337,791	24,776	363,671	2.3
1993	93,399	0	82,080	22,709	104,790	1.1
1994	159,175	0	38,555	15,746	54,301	0.3
1995	25,505	0	4,016	18,660	22,676	0.9
1996	303,703	0	292,225	18,896	311,121	1.0
1997	113,707	171	103,362	29,352	132,885	1.2
1998	59,498	0	188,818	12,532	201,350	3.4
1999	24,035	0	63,699	18,163	81,862	3.4
2000	228,151	0	128,917	8,094	137,011	0.6
2001	132,155	0	35,321	17,468	52,789	0.4
2002	249,095	3,679	171,822	34,998	210,499	0.8
Averages						
1967-2002	202,313	5,224	201,668	31,462	238,353	1.3
1967-1981	227,212	10,910	288,231	28,438	327,579	1.6
1982-2002	184,528	1,162	139,837	33,622	174,620	1.2

¹ The 1977 spawning abundance was discounted from 435,720 to 300,700 spawners based on observed pre-spawning mortality.

Note that the escapements in Table 5 are larger, in recent years, than those in Table 4 because of the inclusion hatchery-origin fish on the spawning grounds.

These data look very similar to those from the Cedar River, which comprises the majority of the spawning and recruitment to Lake Washington. The fits of the Ricker model to the original data are given in Figures 7 and 8. The parameter estimates for 1982-2002 showed a decrease in productivity when compared to those for 1967-1981 (Table 3). The same decrease in productivity observed for Cedar River production was seen in the time series (Figure 9).

The stock-recruit data for the 1982-2002 broods resulted in an estimated \hat{S}_{MSY} of 102,000 spawners for all Lake Washington natural spawning populations (Table 3, Panel A), with a range that would, on average, produce 90% of MSY from 69,000 spawners to 140,000. The 90% confidence interval around \hat{S}_{MSY} was from 66,000 to 162,000 fish. The data for the 1967-1981 broods resulted in an estimated \hat{S}_{MSY} of 171,000 spawners, with a 90% MSY range of 113,000 to 238,000 spawners, and a 90% confidence interval of 114,000 to 429,000.

Simulations to estimate the probability of achieving MSY from the Lake Washington counted catch and escapement data showed that there is a 60% probability of attaining > 90% of MSY between spawning escapements of about 75,000 and 125,000 spawners in Lake Washington, using the 1982-2002 brood year data (Figure 10). This percentage drops to 20% at escapements of about 165,000 spawners. Note that the probability never climbs above 81% because of the relatively poor fit of the data.

All Lake Washington NOR sockeye using Ballard Lock data

As noted by Ames (2006), the percentage of the Lock count estimates accounted for by summing freshwater catches and escapement estimates has declined, from 92% in earlier years to 73% from 1992-2007. We constructed two S-R data sets from the Lock count data to determine if any differences were found compared to the Cedar and Lake Washington results. In the first case, “spawners” were estimated by subtracting freshwater catches and hatchery brood stock from the Lock count estimates. Freshwater production of NORs was estimated by subtracting hatchery production from the Lock count, in 1995-2007. Estimated marine harvest of NORs was added to freshwater production to estimate the number of total annual NORs. Case #1 then assumes that the Lock count is accurate and no mortality occurs in freshwater, thus all fish not caught after passing the Locks survive to spawn.

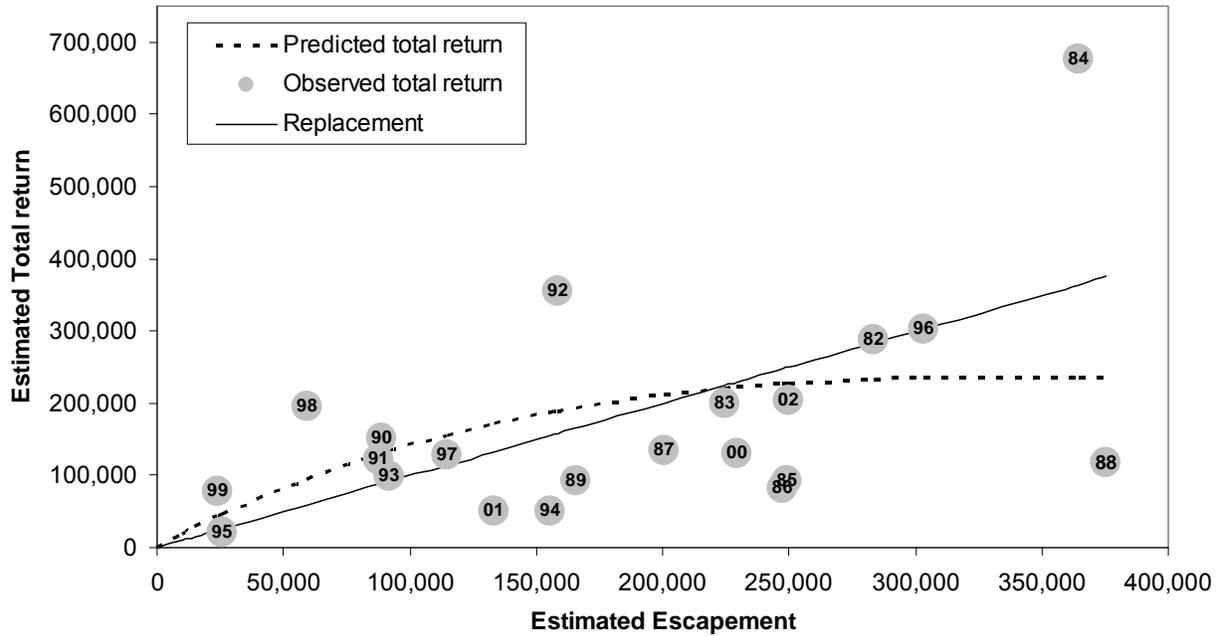


Figure 7—Estimated production of adult sockeye salmon of natural origin from Lake Washington in brood years 1982-2002 against the estimated escapement, along with curves corresponding to least-squares fit of the Ricker model and the replacement line.

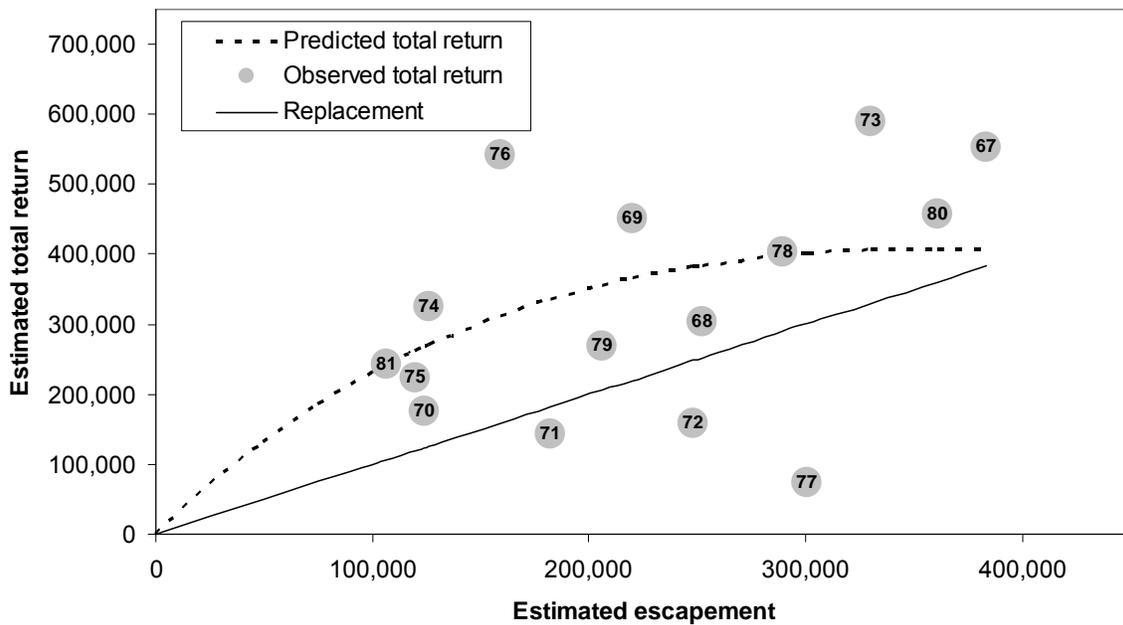


Figure 8—Estimated production of adult sockeye salmon of natural origin from Lake Washington in brood years 1967-1981 against the estimated escapement, along with curves corresponding to least-squares fit of the Ricker model and the replacement line.

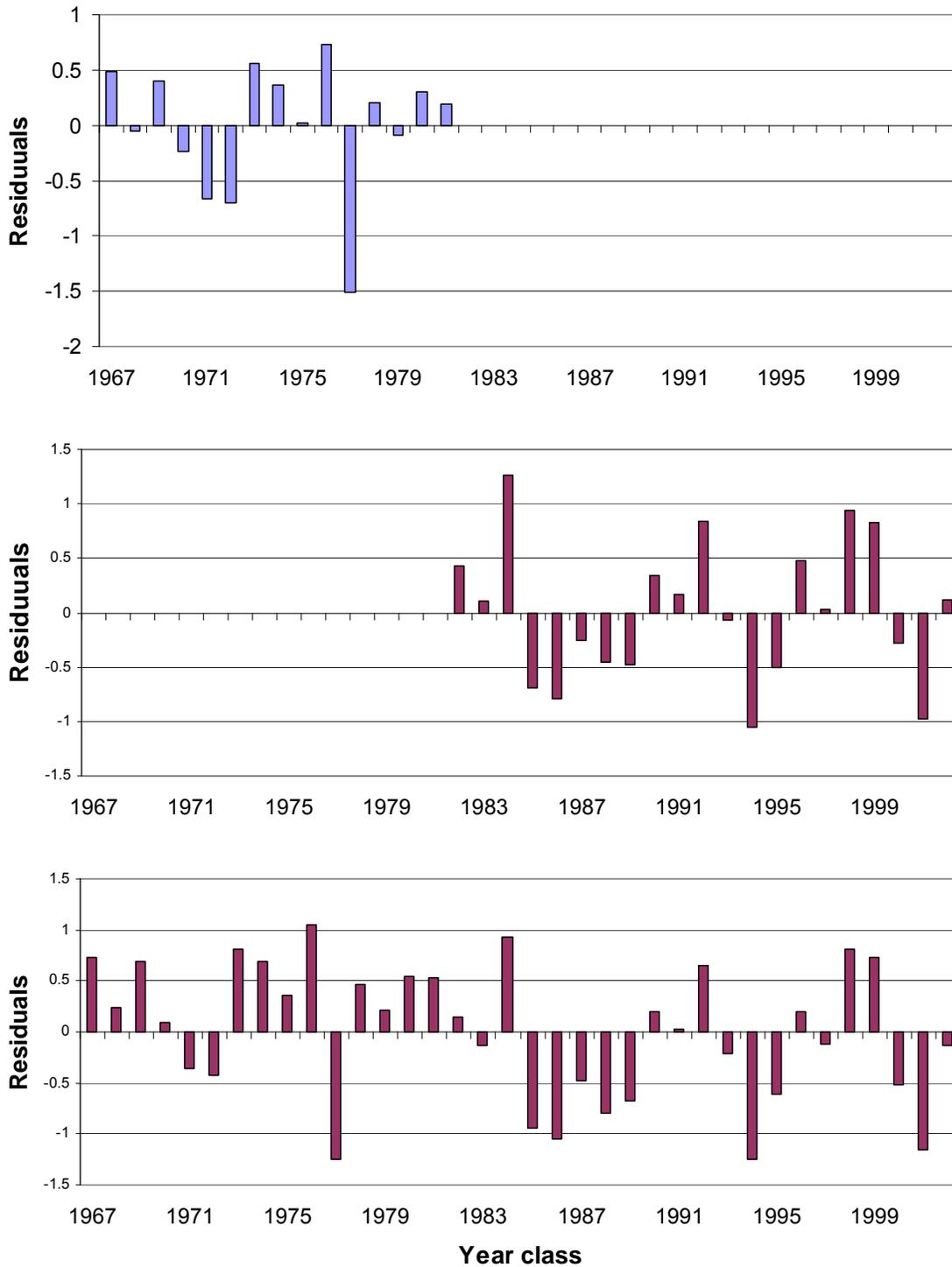


Figure 9—Estimated residuals of the log-transformed fit of the Ricker model to production of sockeye salmon of natural origin from Lake Washington for three fits of the 1967-2002 brood years. The top and middle panels are residuals to the fit for those broods only.

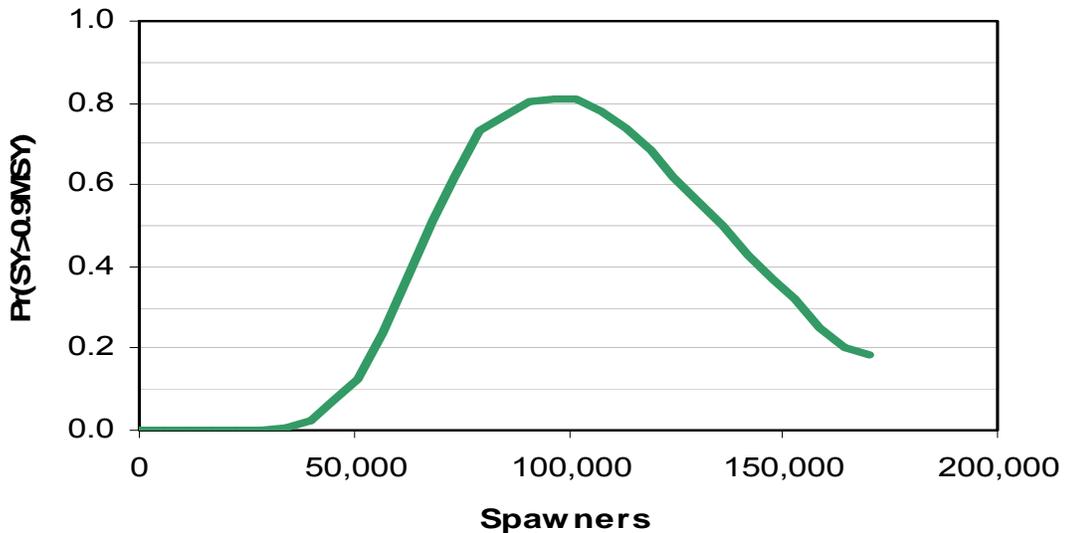


Figure 10—Probability that a specified spawning abundance will result in sustained yield exceeding 90% of maximum sustained yield for Lake Washington sockeye salmon (counted catch and escapement), brood years 1982-2002.

In the second case (case #2), the observed escapements from all spawning areas, used in the section above, were the spawning stock. Recruits were the estimated Lock count plus marine harvest of NORs. Case #2 assumes that the Lock count is accurate, the escapement estimates are accurate and that any fish unaccounted for after passage into freshwater die prior to reaching the spawning grounds. These two Lock-based data sets are presented in Table 6.

Results from case #1 of the Lock analysis differed somewhat from those for the Lake Washington dataset in Table 3. The estimated \hat{S}_{MSY} was 116,000 (14,000 fish higher) with a 90% MSY range of 78,000 to 159,000, for the 1982-2002 broods. Some parameter estimates were similar such as the low exploitation rate at MSY (33%), and S_{MAX} was still greater than S_{EQ} . However, the decrease in productivity was less pronounced and the pattern of residuals more stable for the entire time series (Figure 11). In case #2, the estimated \hat{S}_{MSY} was slightly higher (120,000—see Table 3) and the pattern of residuals was almost as good as those seen in case #1 (Figure 12). The estimated exploitation at MSY was higher (44%) because of the addition of fish in returns, presumed to have suffered mortality after Lock passage.

Table 6—Estimated parents (spawners) and adult recruits of sockeye salmon of natural origin from all Lake Washington stocks for brood years 1967-2002, using Lock-count escapements and returns (Case 1) and all counted escapements and Lock-based returns (Case 2).

Year	Case 1— Lock escapement and returns		Case 2—Counted esc. and Lock returns	
	Escapement (S)	Total (R)	Escapement (S)	Total (R)
1967			383,250	553,546
1968			252,000	304,437
1969			220,000	437,216
1970			124,000	220,373
1971			182,201	187,968
1972	207,422	203,088	248,448	203,088
1973	314,848	520,114	329,904	520,114
1974	170,182	287,638	125,919	287,638
1975	164,055	233,695	119,811	233,695
1976	213,236	584,680	159,209	584,680
1977	358,998	125,589	300,700	125,589
1978	253,886	500,974	289,583	500,974
1979	217,777	341,090	205,800	341,090
1980	369,599	439,427	360,749	439,427
1981	194,518	260,502	106,602	260,502
1982	346,333	275,082	289,774	275,082
1983	344,873	182,923	229,671	182,923
1984	342,746	677,958	372,525	677,958
1985	277,949	110,905	253,135	110,905
1986	240,616	101,704	251,061	101,704
1987	176,333	162,734	204,705	162,734
1988	358,366	176,730	377,806	176,730
1989	193,671	125,955	166,972	125,955
1990	119,895	160,716	93,825	160,716
1991	84,278	140,748	87,952	140,748
1992	239,023	423,508	159,247	423,508
1993	125,516	119,198	93,399	119,198
1994	161,207	71,380	159,175	71,380
1995	30,435	45,103	25,505	45,103
1996	391,389	387,101	303,703	387,101
1997	120,833	208,746	113,707	208,746
1998	83,002	274,917	59,498	274,917
1999	50,026	120,336	24,035	120,336
2000	325,824	236,722	228,151	236,722
2001	257,203	70,135	132,155	70,135
2002	315,345	328,260	249,095	328,260
Averages				
1967-1981	246,452	349,680	236,213	346,689
1982-2002	218,327	209,565	184,528	209,565

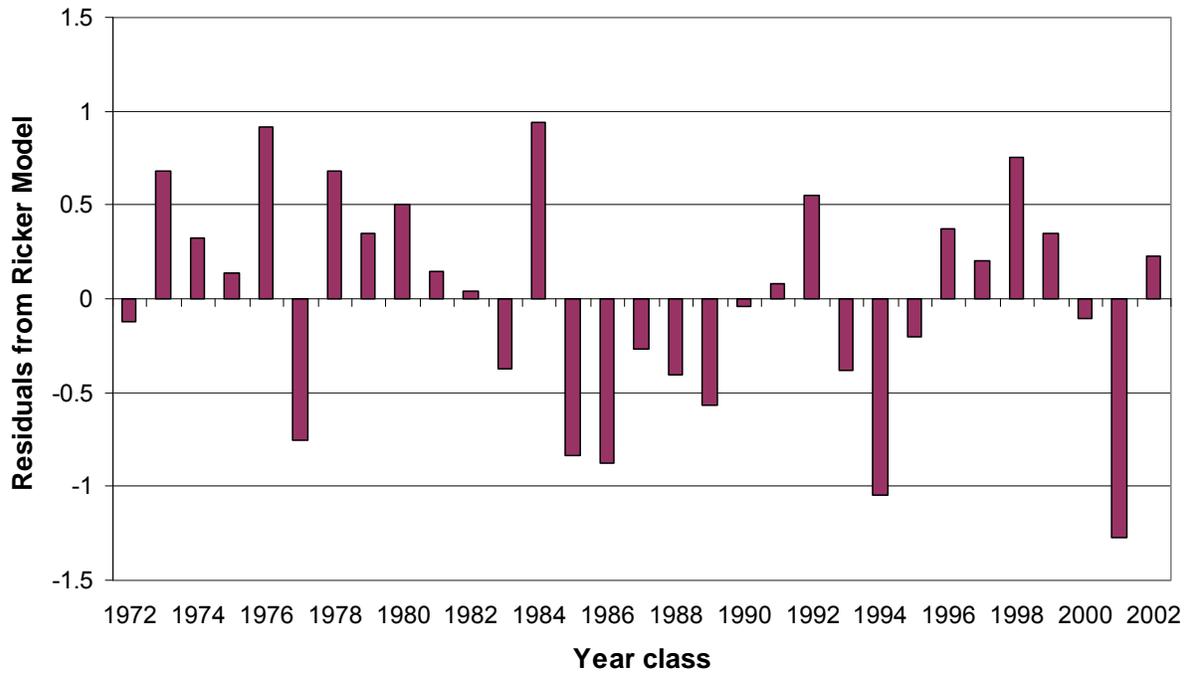


Figure 11—Estimated residuals of the log-transformed fit of the Ricker model to production of sockeye salmon of natural origin from Lake Washington, using Lock counts minus harvest to estimate escapement for the 1972-2002 brood years.

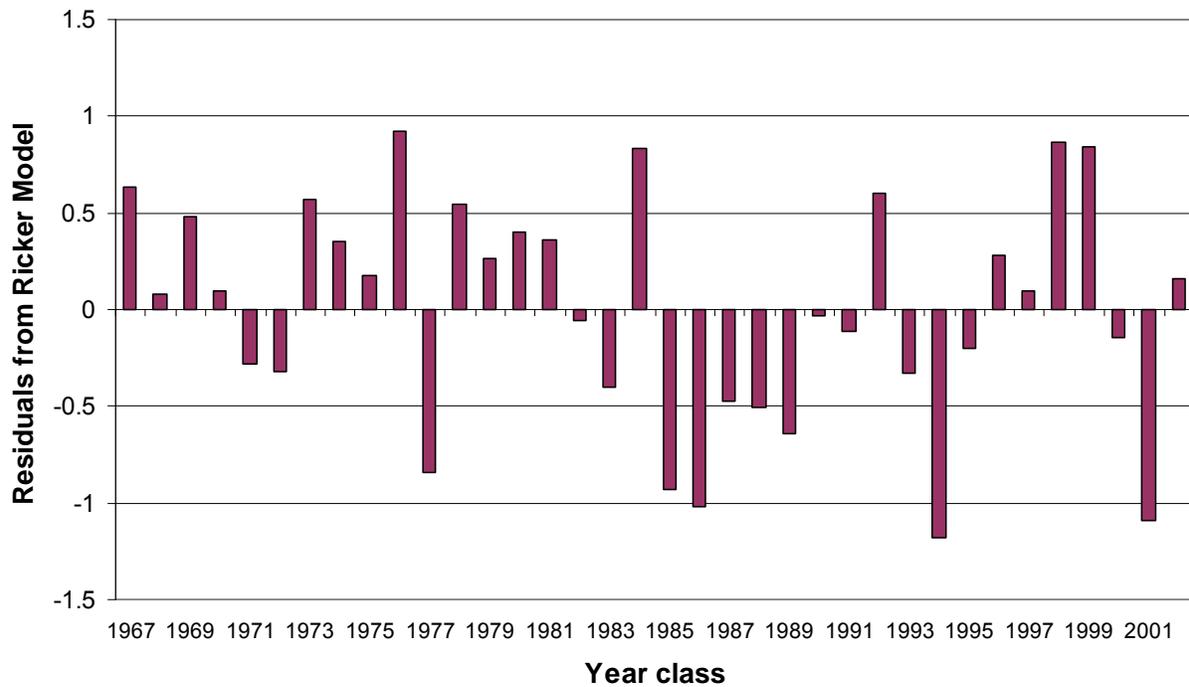


Figure 12—Estimated residuals of the log-transformed fit of the Ricker model to production of sockeye salmon of natural origin from Lake Washington, using Lock counts plus marine harvest to estimate recruitment for the 1967-2002 brood years.

We recognize that the percent of the Lock count estimate accounted for by adding escapement to harvest has decreased, but this does appear to have bearing on production estimates, including the estimate of \hat{S}_{MSY} .

Analysis of even- and odd-year broods

We examined the S-R relationships for even-year broods separately from odd-year broods to assess a pattern of recruitment variation observed in the data. Analyses were conducted on two data sets: the Lake Washington “catch + escapement” accounting method for recruitment (Table 5) and the case #2 accounting wherein Lock counts plus marine harvest were used for the recruitment estimates, while escapements were the same as those in Table 5.

There was a striking difference in results between even- and odd-year broods and between time periods (Table 7). For example, the estimated even-year \hat{S}_{MSY} values for the Lake Washington escapement to Lock recruit data were relatively stable: 150,400 for all even-year broods, 146,000 for 1982-2002 and 165,000 for 1968-1980. Parameter values were significant and residual patterns stable for all three runs of this data (Figures 13 and 14). The exploitation rates estimated for MSY were very stable, 0.52, 0.50 and 0.53. For the odd-year brood years, parameter values were significant (except for 1967-1981) but residual patterns were not stable; S_{MSY} values varied with time and were estimated at 135,000 for all odd-year broods, 69,500 for the 1983-2001 broods, and 184,000 for the 1967-1981 broods.

Using the Lake Washington “catch + escapement” data produced similar results, but two-thirds of the fits were poor (non-significant parameter values, etc.). The S_{MSY} estimates for even-year broods ranged from 129,300 to 160,000 (—see Table 7) and were similar to values for the Lock recruit data set. The S_{MSY} estimates for the odd-year broods were similar to those above, 60,000 for the 1983-2001 broods to 191,000 for the 1967-1981 odd-year broods.

Simulations to estimate the probability of achieving MSY from the Lake Washington escapement to Lock + marine harvest data for the even-year broods (1968-2002) showed that there is a 60% probability of attaining > 90% of MSY between spawning escapements of about 100,000 and 190,000 spawners in Lake Washington (Figure 15). This percentage drops to 20% at escapements of about 25,000 spawners. Note that the probability peaks at 89% and the left side of the curve is steeper, compared to Figures 6 and 10, because of the better fit of the data to the Ricker Model.

Table 7—Parameter estimates from the log-linear transform of Ricker’s model on estimates of adult production and spawning abundance of Lake Washington sockeye salmon of natural origin for odd- and even-year broods, using two data sets (counted catch and escapement, and counted escapement and Lock recruitment) and analysis of the 1982-2002, 1967-1981 and 1967-2002 brood years.

Time Series	1982-2002 (Even)	1983-2001 (Odd)	1982-2002 (Even)	1983-2001 (Odd)
Data	Lake Wa Catch & Esc ¹	Lake Wa Catch & Esc ¹	Lake Wa Esc vs. Lock Recruit ²	Lake Wa Esc vs. Lock Recruit ²
\hat{S}_{MSY}	130,100	60,000	146,000	69,500
\hat{R}_{MSY}	230,000	88,000	294,000	150,000
\hat{U}_{MSY}	0.43	0.34	0.50	0.53

Time Series	1968-2002 (Even)	1967-2001 (Odd)	1968-2002 (Even)	1967-2001 (Odd)
Data	Lake Wa Catch & Esc ¹	Lake Wa Catch & Esc ¹	Lake Wa Esc vs. Lock Recruit ²	Lake Wa Esc vs. Lock Recruit ²
\hat{S}_{MSY}	139,400	141,200	150,400	135,100
\hat{R}_{MSY}	269,000	198,000	315,000	228,000
\hat{U}_{MSY}	0.48	0.28	0.52	0.40

Time Series	1968-1980 (Even)	1967-1981 (Odd)	1968-1980 (Even)	1967-1981 (Odd)
Data	Lake Wa Catch & Esc ¹	Lake Wa Catch & Esc ¹	Lake Wa Esc vs. Lock Recruit ²	Lake Wa Esc vs. Lock Recruit ²
\hat{S}_{MSY}	160,000	191,000	165,000	184,000
\hat{R}_{MSY}	335,000	348,000	358,000	316,000
\hat{U}_{MSY}	0.52	0.44	0.53	0.45

¹ Results obtained from data in Table 5.

² Results obtained from data in Table 6, Case 2.

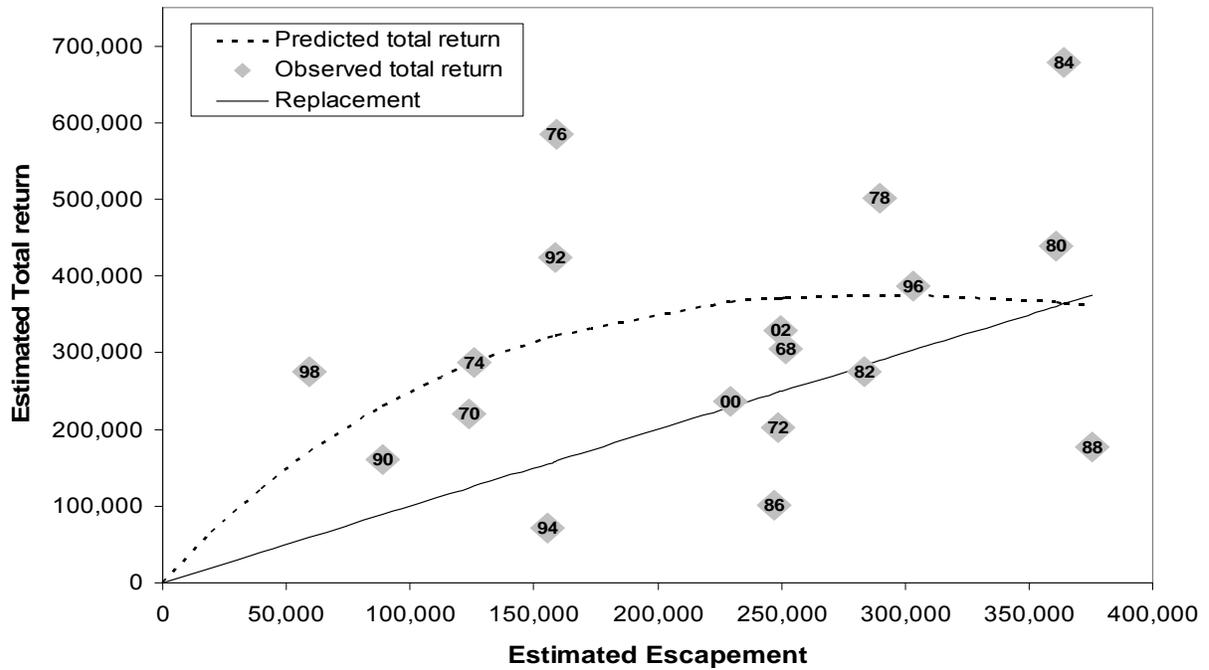


Figure 13—Estimated production (Lock Count + marine harvest) of natural origin sockeye salmon in Lake Washington in brood years 1968-2002 (even-year broods) against the estimated escapement, along with curves corresponding to least-squares fit of the Ricker model and the replacement line.

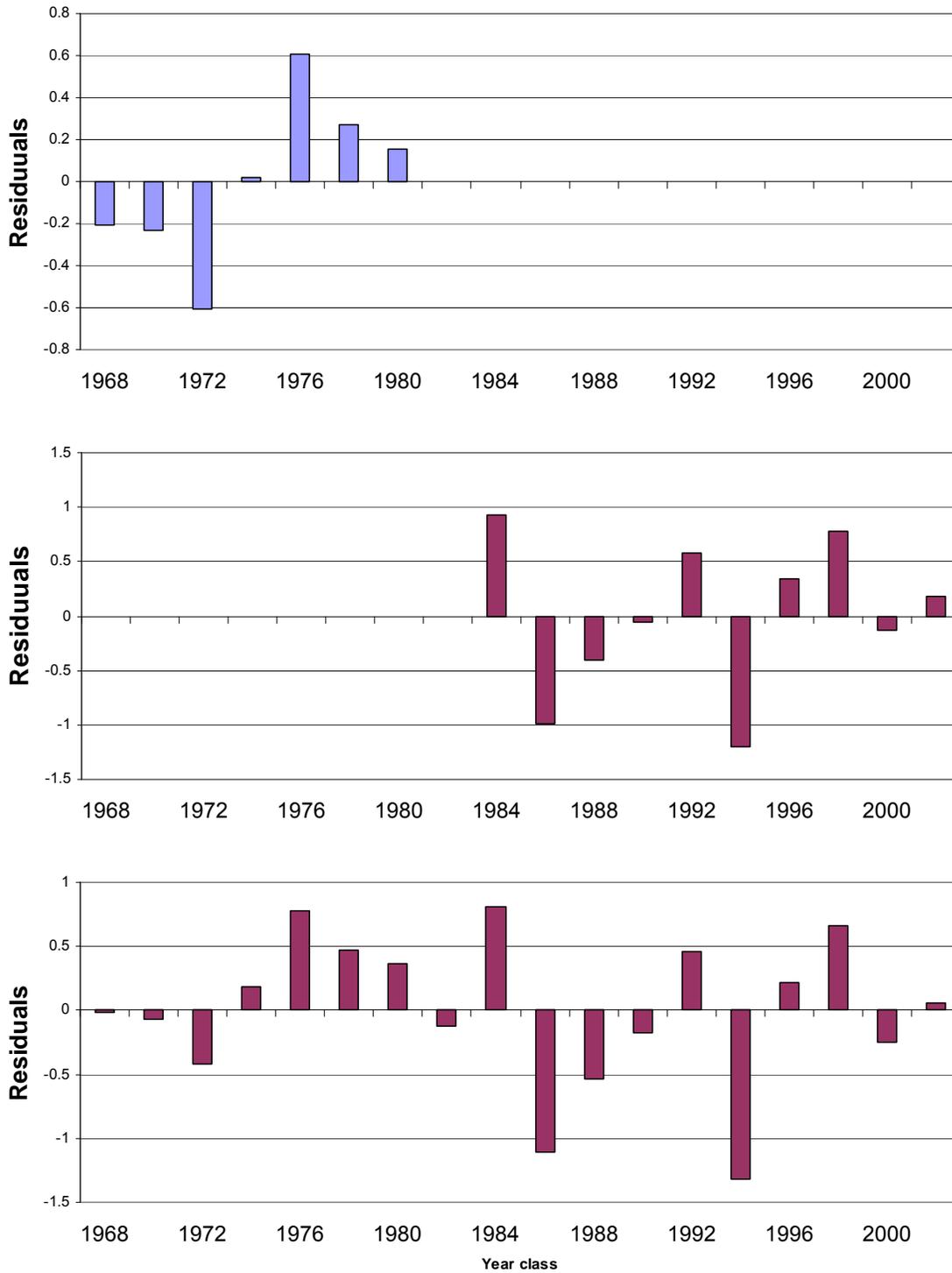


Figure 14—Estimated residuals of the log-transformed fit of the Ricker model to production of adult sockeye salmon of natural origin from Lake Washington for three fits of the 1968-2002 even-year broods, using estimated escapements against Lock Count returns + marine harvest from Table 6.

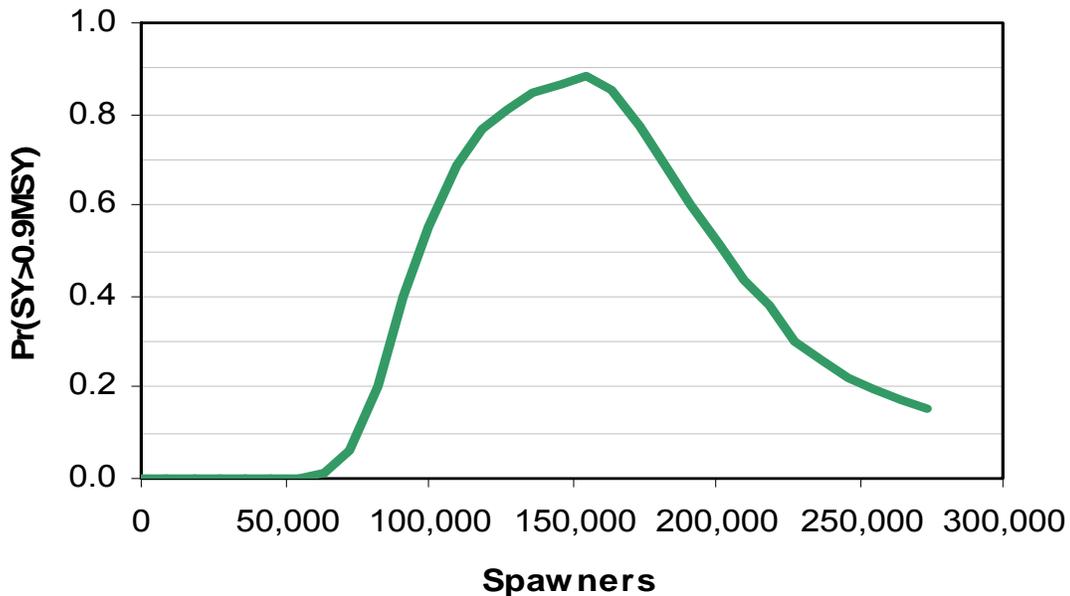


Figure 15—Probability that a specified spawning abundance will result in sustained yield exceeding 90% of maximum sustained yield for Lake Washington sockeye salmon (counted catch and escapement), brood years 1982-2002.

We had more confidence in the Lock Recruit data set overall, but both data sets point to the same results: 1) a reasonably stable production regime for even-year broods years since 1967, and 2) a pronounced decreasing production trend for odd-year broods. We conclude that the S_{MSY} for even-year broods is approximately 150,000 natural spawners. For the odd-year broods, productivity will likely remain low unless there is a reversal of the events leading to the decline in the early 1980s. If production remains low, fishing opportunities will remain scarce.

Comparison of Cedar River to non-Lake Washington sockeye BRPs

Evaluation of stock-recruitment (S/R) relationships and productivities of non-Lake Washington sockeye stocks in Washington and southern British Columbia may provide insight into the assessment of Cedar River sockeye BRPs. Spawner abundance and recruitment data sets for eight stocks (i.e., *reference stocks*) were obtained and analyzed for relevant parameters commonly used to assess productivity and escapement/harvest policy.

Stocks

Selection of sockeye stocks that would provide comparisons with Cedar River sockeye is made difficult by the environment occupied by the latter. While the Cedar River watershed may not differ greatly from other watersheds that support spawning sockeye in coastal areas, the river flow is regulated to some degree for municipal water supply and flood control. More importantly, Lake Washington should be considered unique in its biological characteristics and ecology as pertaining to juvenile sockeye. Age 1 sockeye salmon smolts emigrating from Lake Washington are among the largest in the world. Given that we would not likely be able to assemble data from strictly comparable stocks, we deemed that the most practical approach to assessing Cedar River/Lake Washington sockeye productivity would come from analyses of stocks in the same geographical area.

In order to make valid comparisons between Cedar River sockeye and sockeye found in other watersheds of Washington and southern British Columbia, we reasoned that these other stocks should mimic, as far as possible, the basic biological characteristics of Cedar River sockeye. First, we eliminated from consideration many Fraser River sockeye stocks that exhibit cyclical dominance. These stocks generally show some degree of inter-cohort effects (interaction between adjacent brood years), a feature not found in Cedar River sockeye.

Second, an obvious need in the analysis was the availability of sufficient numbers of brood years of reliably collected spawning stock and recruitment data. Data quality on one or both measures of abundance likely varies between and within stocks, but the scope of this examination precludes extensive evaluation of the datasets. Sufficient time-series of data ($n = 23$ to 53 brood years) were available for the reference stocks while we used the most recent 21 years of Cedar River S-R data (1982-2002 brood years) used in our analyses. In addition, we eliminated from consideration stocks that are enhanced via fry recruitment assistance.

The stocks chosen for this comparison were Lake Quinault sockeye in Washington, Sproat Lake and Great Central Lake sockeye in the Barkley Sound area on the west coast of Vancouver Island, British Columbia, and Cultus, Birkenhead, Fennell, Raft and Stellako sockeye stocks of the Fraser River system, British Columbia. These eight reference stocks are either non-enhanced stocks (Quinault, Sproat, Cultus, Birkenhead, Fennell, Raft and Stellako), or enhanced only by nutrient additions to the rearing lake (Great Central) for the period of data.

Counts or estimates of arriving fish and or, spawning ground escapement estimation programs provide the management agency with estimates of annual spawning population size. Recruitment is obtained by summing the estimates of catch

in the various fisheries conducted on the migration routes and in the terminal area for each stock. Various means of allocation of non-terminal area catch to stock of origin are used. Allocation via proportional escapement and age composition data (Great Central and Sproat) provides robust estimates by stock wherein stocks are thoroughly mixed. Analysis of stock composition via racial analyses using biological and/or genetic information has been used by the Pacific Salmon Commission to allocate catch between stocks within the Fraser River drainage (Gable and Cox-Rogers 1993).

Uncertainties in the data sets, if large, may invalidate conclusions regarding the parameters estimated by the available data for individual stocks. Measurement error should be random, but may bias certain estimates. For Cedar River sockeye, the uncertainty regarding the abundance of spawning sockeye utilizing the lower portion of the river in recent years may introduce a directional bias since assumptions regarding the AUC estimates of escapement may be violated by hypothesized shortened redd life. Changes in data collection procedures may cause between-year variation in estimates and result in biased parameter estimates. The averaging of eight stocks should negate the potential impact of significant measurement error in individual stocks.

Stock-recruitment models

Salmon managers have examined a number of means to characterize populations in meaningful ways to obtain comparable statistics. We used as our default assumption that the suite of stocks we analyzed would each fit the Ricker Stock-Recruitment relationship (Ricker 1975).

First, we examined the S-R data available for adherence to Ricker S/R model assumptions. Linearity in the relationship between the natural logarithm of the recruitment rate and adult escapement by year was examined as:

$$\ln(R_y) - \ln(S_y) = \ln(\alpha) - \beta S_y + \varepsilon_y.$$

We plotted the residuals of the observations to ascertain if violations to the assumption qualitatively appeared severe enough to reject the assumption. All the selected stocks appeared to meet this first requirement.

Secondly, we examined the potential for inter-cohort effects on the recruitment. Our objective was to isolate potential cycle-line effects that would violate assumptions of the Ricker S-R relationship (Woodey et al. 2005). We looked for significance in the effects of escapements one and two years prior to the brood year in question via multiple regression wherein:

$$\ln(R_y) - \ln(S_y) = \ln(\alpha) - \beta_1 S_y + \beta_2 S_{y-1} + \beta_3 S_{y-2} + \varepsilon_y.$$

All of the stocks in the present list showed non-significant effects of immediate prior year escapements.

Next, we fit the Ricker Curve and calculated bias corrected S-R parameters (Hilborn and Walters 1992) including the Ricker “a” value, S_{max} , S_{msy} , S_r , R at S_{max} , R/S at S_{max} , R/S at S_{msy} , R/km^2 of lake surface area at S_{max} and S_{msy} and harvest rate (HR) at S_{msy} . This suite of parameters provided information on which comparative analyses were based. Three parameters (Ricker “a” value, R/km^2 of lake surface area at S_{max} and HR at S_{msy}) have been used to characterize the sockeye stocks that we examined for comparison with the Cedar River stock parameter values.

Results

The assessment of Cedar River sockeye BRPs relative to the eight reference stocks (Table 8) indicated that sufficiently large differences existed between measures of productivity that uncertainty and bias in datasets should constitute a small portion of the observed differences.

The graph of the relationship between $\ln(R/S)$ vs. spawners for Cedar River sockeye (Figure 2) shows that, for the 21-year (1982-2002) period, recruitment exceeded the brood year escapement in seven years while it was less than the escapement in twelve years and equal in two years. In sum, the 3,251,000 spawners in the period produced 2,966,000 recruits, a loss of 285,000 fish. When catch is removed, the escapement profile in the late 1980s to present shows a decline (Figure 1) relative to the earlier period.

Stock-recruitment parameter estimates for Cedar River sockeye and the eight reference stocks (Table 8) provide a snapshot of productivity estimates and sustainable harvest rates for stocks that display non-cyclical production.

Ricker “a” value

The Ricker “a” value is taken as a measure of the productivity of a population, i.e., it is the bias-corrected intercept of the regression of $\ln(R/S)$ vs. spawner abundance and approximates the recruitment rate as spawner abundance approaches 0. In Cedar River sockeye, the Ricker “a” value was calculated at 1.91 (Table 8). The values obtained from the eight reference stocks ranged from 4.13 (Quinalt) to 17.26 (Sproat), and averaged 8.70 (geo. mean). This statistic indicates that the Cedar River sockeye are very unproductive, or that the recruitment relationship is very flat, i.e., little change over a wide range of spawner abundance. The data did not support the latter possibility.

Table 8— Comparative bias-corrected Ricker stock-recruitment model parameters for sockeye stocks and optimum adults per lake area.

Watershed	Lake	Sockeye		Lake Area		Ricker "a"	at S _{max} R/km ²	HR at S _{msy}
		Stock	Years	(km2)				
Lake Washington	Lake Washington	Cedar River ¹	21	88	1.91	2,239	30%	
	" "	All stocks ²				2,624		
Lake Quinault	Quinault	Quinault	26	15.1	4.13	3,887	57%	
Fraser River	Harrison	Birkenhead	51	220	13.19	3,423	83%	
	" "	All stocks ³				5,733		
	Cultus	Cultus	47	6.3	6.98	16,825	71%	
	N. Barrier	Fennell	29	5.2	13.22	9,558	83%	
	Kamloops	Raft	49	56	7.15	1,857	71%	
	" "	All stocks ³				2,044		
	Fraser	Stellako	53	54	8.40	16,352	75%	
Barkley Sound	Great Central	Great Central	23	51	6.30	9,431	69%	
	Sproat	Sproat	23	41	17.26	12,561	86%	
Average of eight reference stocks:		adj. Mean =			9.58	9,549	74%	
		geo. Mean =			8.70	7,834	74%	

¹ Natural spawning Cedar River sockeye only, 1982-2002 data.

² Estimated by division using mean proportion: Cedar River of total Lake Washington escapement (w/o L. Sammamish populations).

³ Estimated by division using mean proportion of reference stock:total lake escapement.

Lake capacity

Limitations to sockeye salmon production in river-lake systems stem from two different sources: spawning ground capacity and lake rearing capacity. Generally, one can deduce the cause of the limitation by assessing measures of lake size, morphology and primary productivity relative to the stream and lake beach areas available for spawning. Competition and predation in the limnetic zone of lakes also affect capacity for growth and survival of juvenile sockeye. Lake capacity estimates as measured by Cedar River spawner density and recruitment at S_{max} is informative, but without adjustment for the abundance of other stocks of sockeye that utilize the Lake Washington (i.e., excluding L. Sammamish), may be misleading. Within Lake Washington, Cedar River sockeye have accounted for approximately 85.3% (1982-2002 range: 68-98%; SD = 7.8%) of sockeye estimated to have spawned annually in the watershed. "Adjustment" of the estimates of Lake Washington capacity has been made by application of the Cedar River percentage contribution. Likewise, we adjusted spawning stock and recruitment estimates at S_{max} for two Fraser watershed lakes (Harrison and Kamloops). Other lakes have only one stock or the escapements have been combined in this analysis.

At S_{max} , Lake Washington recruitment productive capacity was estimated at 2,624 fish/km² vs. a geometric mean of 7,834 fish/km² (range: 2,044 -16,825; Table 8) for the reference lakes. Given historically high juvenile growth rates (Overman et al. 2006) and low recruitment/km² at S_{max} , this comparison suggests either spawning ground limitations or high in-lake mortality rates that lead to low productivity of Lake Washington sockeye.

Harvest rate

At S_{msy} , the average harvest rate for Cedar River sockeye was estimated at only 30% (Table 8), while at S_{max} the stock could not be fished because the average recruitment (197,000 fish) was less than the escapement (280,000 spawners) required to produce that size run (Table 3, Panel A). In comparison, the suite of reference stocks gave a geometric mean harvest rate of 73% at S_{msy} . Again, Cedar River sockeye are unproductive relative to a suite of other stocks. This is not to say that there are not other unproductive sockeye stocks, just that compared to stocks that are actively managed, and for which data series are available, Cedar River fish have been very unproductive in the recent time period.

In all comparisons between Cedar River NOR sockeye and a suite of non-Lake Washington stocks, Cedar River sockeye show distinctly lower values in measures of productivity. However, this analysis could not provide insight into the causes of the lower productivity.

Examination of mechanisms controlling Cedar River sockeye recruitment

As evidenced by the results of the S-R analyses, Cedar River and total Lake Washington sockeye populations are relatively unproductive, i.e., the MSY escapement estimates and the harvest rates at MSY are low in comparison with other sockeye stocks in the region. In order to try to account for the low productivity and to try to identify the causes of the lower productivity in the more recent time period, we examined relationships within the fry and juvenile database along with data from other sources. Herein we present our analysis and propose hypotheses regarding the mechanisms controlling fry survival that may provide insight into the bottlenecks that the stock now faces, and ultimately, guidance to the managers in their deliberations regarding escapement policy.

Estimates of survival between life stages

We first examined the data collected in studies on Cedar River and Lake Washington sockeye salmon over the past 40+ years. While no dataset has been collected using consistent methodology over the entire period, we have used most of the available data after examination for obvious inconsistencies. Our objective here is to provide an analysis of the data before moving to the development of hypotheses regarding the mechanisms affecting productivity of the stocks.

Cedar River NOR egg to fry survival

Fry trapping in the lower Cedar River began in 1992 to assess natural origin fry abundance and the recruitment of hatchery fry released into the river to supplement the natural fry abundance. Cedar River natural fry production in the 1991-2007 brood years varied between 0.7 and 38.7 X 10⁶ fry (Table 9), corresponding to survival rates of potential eggs carried into the Cedar River by females to fry emergence of 1.9 to 32.0%. The mean natural fry production has been 20.6 X 10⁶ fry while the mean egg to fry survival has been 13.5%. Estimated survival rate from eggs in to fry out is within normal variation observed in the Washington/southern British Columbia region and is close to the average (14.1%; n=3) observed in Adams River, British Columbia (Williams et al. 1989).

Natural fry production has varied relative to three significant factors: spawning population size effects (positive), effects of spawning period (October 15-November 15) minimum flows (Qmin) (positive) and effects of incubation period (November through February) maximum flows (Qmax) (negative). A multiple regression relationship of fry abundance vs. these three factors explains much of the variation in natural fry recruitment (1991-2007 BY: adj. R² = 0.838**; n=17). A portion of the remaining variance may be associated with spawner parameter measurement error (spawner number, sex ratio, egg retention, etc.) and to variable effects of environmental

Table 9—Estimated fry recruitment of Cedar River sockeye from natural spawners and river flow parameters, for brood years 1991-2007.

Brood Year	NOR spawning and fry		Natural Fry (10*6)	Egg-fry survival %	Natural fry-adult survival %	Hatchery fry @ trap (10*6)	Total Fry (10*6)	Cedar River Qmin cfs @ peak spawn	Cedar River Qmax (cfs) Nov-Feb
	Spawners	PED est. (10*6)							
1991	77,000	126.36	9.80	7.76%	1.00%	0.60	10.40	316	2,060
1992	100,000	173.50	27.10	15.62%	1.05%	1.70	28.80	324	1,570
1993	76,000	117.57	18.10	15.39%	0.48%	6.60	24.70	346	927
1994	109,000	173.09	8.70	5.03%	0.48%	5.60	14.30	255	2,730
1995	22,000	38.13	0.73	1.91%	2.18%	5.10	5.83	439	7,310
1996	230,000	379.27	24.39	6.43%	0.87%	13.90	38.29	311	2,830
1997	104,000	171.18	25.35	14.81%	0.42%	7.60	32.95	368	1,790
1998	49,588	78.75	9.50	12.06%	1.48%	9.02	18.52	300	2,720
1999	22,138	39.75	8.06	20.28%	0.90%	2.01	10.07	388	2,680
2000	148,225	255.76	38.45	15.03%	0.29%	13.51	51.96	416	627
2001	119,000	212.30	31.67	14.92%	0.13%	11.97	43.64	439	1,930
2002	194,640	330.40	27.86	8.43%	0.59%	14.41	42.27	325	1,410
2003	110,404	188.35	38.69	20.54%		9.22	47.91	404	2,039
2004	116,978	191.61	37.03	19.33%		13.65	50.68	422	1,900
2005	50,887	77.98	10.86	13.93%		4.24	15.10	406	3,860
2006	106,961	155.60	9.25	5.94%		10.32	19.57	364	5,411
2007	45,489	78.5	25.07	31.95%		2.50	27.57	417	1,820
Average	98,959	169.35	20.62	13.49%	0.82%	7.76	28.39	367	2,566

conditions during spawning and incubation, e.g., timing and number of high water events, etc.

Fry to presmolt survival

Annual hydroacoustic estimates of March presmolt sockeye abundance are available for the 1967-1988, 1991-1994 and 2000-2005 brood years. However, fry abundance estimates are only available beginning with the 1991 brood, thus we are restricted to this period for analysis of fry to presmolt survival. The data for the 1991-1994 brood period showed an average of 22.87×10^6 fry (range: $12.4-33.2 \times 10^6$) for all natural plus hatchery populations contributing fry to Lake Washington (i.e., excluding Lake Samammish populations) and an average of 1.62×10^6 presmolts (range: $0.25-2.18 \times 10^6$), giving a geometric mean survival of 5.73%.

More recent studies on juvenile abundance and distribution in Lake Washington (Overman et al. 2006; Overman and Beauchamp 2006 and 2007) suggest that survival in the first growing season (to surveys in October) and through the winter to March can be highly variable. In the six brood years (2000-2005) for which complete abundance data are available (Table 10), the total fry recruitment estimates varied by a factor of 3.5 ($16.4-56.6 \times 10^6$ fry; mean = 44.8×10^6), but October juvenile abundance estimates varied by a factor of 18.7 from 0.14 to 2.62×10^6 juveniles (mean = 1.15×10^6) and March presmolt abundances varied by a factor of 19.1, from 0.16 to 3.05×10^6 (mean = 1.62×10^6) presmolts. The geometric mean survival estimate from fry to presmolts was 2.91%. Thus, the near doubling of the fry abundance from 1991-1994 to 2000-2005 broods yielded the same mean presmolt abundance, but at a lower survival rate.

The estimates of in-lake survival appear to be very low, although the number of comparative observations in natural systems in Washington and southern British Columbia is limited. Williams et al. (1989) provided estimates of fry to fall juvenile survival in Shuswap Lake, British Columbia, that averaged 14% and Chilko Lake, British Columbia sockeye fry to smolt survival has been estimated at 48.9% (1949-1967 brood years), but with lower egg-to-fry survival rate (Roos, 1991).

We note that annual hydroacoustic estimates of juvenile and presmolt sockeye populations in Lake Washington in recent years may be quite uncertain. While juvenile sockeye were the predominant limnetic fish species in the late 1960's, subsequent growth of the longfin smelt and stickleback populations along with smaller sockeye abundances has lowered the sockeye proportion in the limnetic fish populations and has increased the uncertainty associated with the estimation of juvenile sockeye abundance. Therefore, the use of individual year estimates is not recommended. However, the mean survival of the six most recent years (2.91%) may be reasonable given that the geometric mean survival from presmolt to adult of the three years for

Table 10—Juvenile sockeye salmon abundance, mean net catch and mean length in Lake Washington for the 2000-2006 brood years and adult recruitment (Overman et al. 2006, Overman and Beauchamp 2006 and 2007). Data are incomplete after the 2002 brood year.

Brood year (yr)		Fry into Lake	March BY+1	October BY+1	March BY+2	Fry - presmolt Survival	Adult Recruits	Fry-Adult Survival	Smolt-Adult Survival
2000	abundance	56.60 X 10 ⁶	N/A	2.62 X 10 ⁶	2.13 X 10 ⁶	3.89%	157,056	0.29%	7.37%
	catch/haul			N/A	N/A				
	mean length (mm)			107.5	108.9				
2001	abundance	47.80 X 10 ⁶	4.42 X 10 ⁶	2.26 X 10 ⁶	3.05 X 10 ⁶	6.60%	63,862	0.14%	2.09%
	catch/haul			N/A	N/A				
	mean length (mm)			92.1	99.8				
2002	abundance	46.35 X 10 ⁶	17.80 X 10 ⁶	1.17 X 10 ⁶	0.99 X 10 ⁶	2.18%	276,201	0.61%	27.90%
	catch/haul			10.5	4.6				
	mean length (mm)			107.8	109.9				
2003	abundance	48.30 X 10 ⁶	2.04 X 10 ⁶	0.22 X 10 ⁶	2.24 X 10 ⁶	4.65%			
	catch/haul			1.0	0.4				
	mean length (mm)			91.9	95.0				
2004	abundance	53.20 X 10 ⁶	15.46X 10 ⁶	0.51 X 10 ⁶	1.17 X 10 ⁶	2.29%			
	catch/haul			1.7	3.4				
	mean length (mm)			99.2	113.2				
2005	abundance	16.42 X 10 ⁶	4.67 X 10 ⁶	0.14 X 10 ⁶	0.16 X 10 ⁶	1.01%			
	catch/haul			1.2	1.7				
	mean length (mm)			107.2	111.0				
2006	abundance	29.17X 10 ⁶	15.07 X 10 ⁶	N/A	N/A				
	catch/haul								
	mean length (mm)								
Geo. means =						2.91%	140,412	0.29%	7.55%

which complete data on adult recruitment are available agrees well with the 1967-1988 average of 12.0% (see below).

Presmolt to adult survival

Studies of Lake Washington sockeye presmolt to adult survival have indicated that survival is consistent with that measured for other sockeye stocks given the large size of Lake Washington smolts (Ames 2006). The 1967-1988 brood year mean survival from presmolt to adult was 12.0%. Data from 1991-1994 brood years show a geometric mean survival of 9.8%. However, the presmolt-adult recruit survival estimates were inversely related to fry-presmolt estimates causing extreme values (2.7-49.7%) likely due to presmolt abundance estimation error. Thus, individual estimates cannot be relied on, but the geometric mean appears to be within the previously observed range for short time series data. Overman et al. (2006) and Overman and Beauchamp (2006 and 2007) provide data on the 2000, 2001 and 2002 brood year presmolt estimates that we have used to estimate survival from presmolt to recruits. Survivals were estimated at 10.6%, 2.3% and 31.2%, respectively (mean = 14.7%; geometric mean = 9.1%; Table 10). While individual recent year data may be uncertain, the mean values appear to be within expected ranges given the adult recruitments.

Cedar River NOR fry to adult survival

While the recent annual presmolt abundance estimates in Lake Washington may be somewhat uncertain, the calculations of fry to adult survival should provide reasonable estimates of annual lake-ocean survival which, along with the egg-to-fry survival, captures the overall recruitment dynamics of the populations.

We first examined the fry to adult survival dataset to determine the relationship between NOR fry and HOR fry survival. An obvious inconsistency involving the 1995 brood fry survival estimate was immediately apparent (Figure 16). The 1995 brood estimate of NOR fry was the lowest observed (0.7×10^6) due to extremely high discharge of the Cedar River during incubation (Table 9). The HOR fry abundance was 5.1×10^6 . In the return estimates, the NOR survival estimate (2.13%) was very much higher than that for HOR fry (0.06%). A second inconsistency was that the NOR adult recruitment was estimated to be 79% age 5 fish, one of the two highest fractions of age 5 recruits in the Cedar River dataset (Table 2). We conclude that the 1995 brood NOR recruitment estimate is likely biased, possibly due to age allocation errors involving age 4 NOR recruits in 2000 wherein a small proportion of the large 1996 brood age 4 fish may have erroneously identified as age 5 fish. This did not appear to occur with HOR recruits, possibly because the thermal marking of otoliths is unique for each brood. We removed the 1995 brood year data from the fry-to-adult dataset prior to subsequent

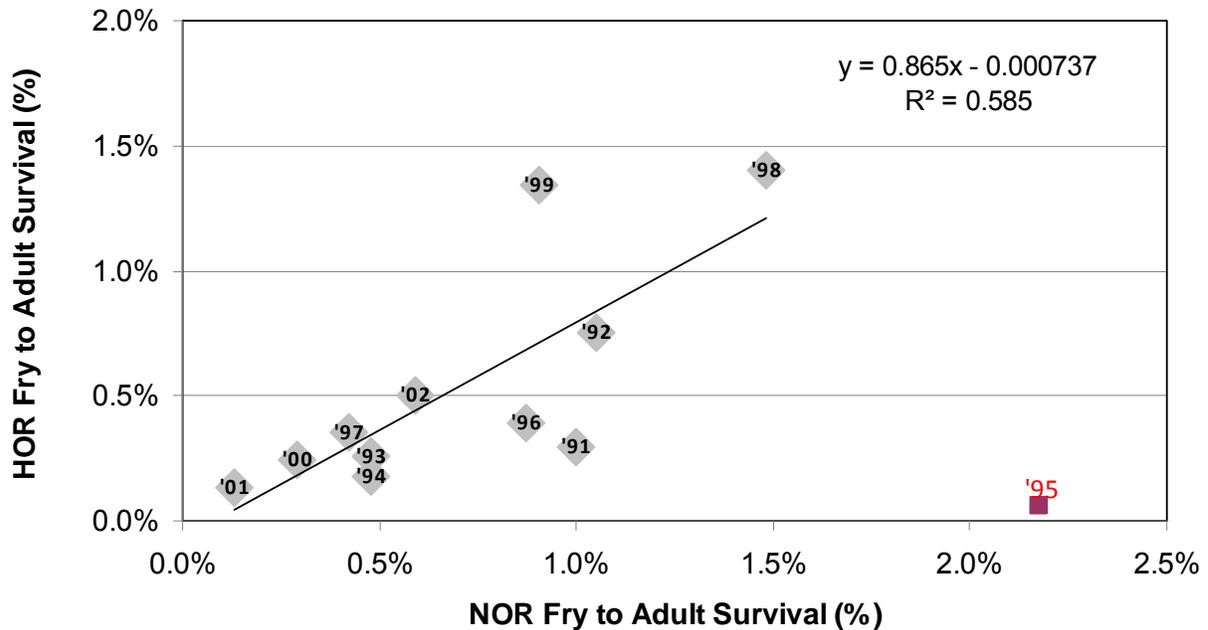


Figure 16—Hatchery-origin Cedar River sockeye fry to adult survival vs. natural-origin fry survival.

analyses. The remaining eleven years of fry-to-adult survival estimates produced a reasonably good fit between NOR and HOR fry (Figure 16: adj. $R^2 = 0.585$; $n = 11$). In general, natural and hatchery Cedar River fry survivals follow a similar pattern within a year, indicating that the mechanism controlling survival affects both groups despite slightly different lake entry timing.

Next, we plotted the NOR survival estimates against NOR fry abundance. The data indicated that even-year brood NOR fry tended to have higher survival than odd-year brood fry at a given fry abundance, particularly at high fry abundance (Figure 17). While the datasets for even- and odd-year broods were inadequate for statistical confidence ($n = 6$ and 5 observations, respectively), it appears that fry-to-adult survival differences in the 1991-2002 period mimic the differences in recruitment rate between even-year vs. odd-year broods observed in the S-R analyses that have a more extensive period of record. Regression of the limited fry survival data showed a lack of major overlap (1994 data is the exception) supporting the notion that a fundamental difference exists between even- and odd-year broods that warrants further examination.

We regressed the HOR fry survival on abundance by even- and odd-year broods, again omitting the 1995 data point (Figure 18). The scatter of the data and overlap between even- and odd-year broods were greater, but again, the general pattern of

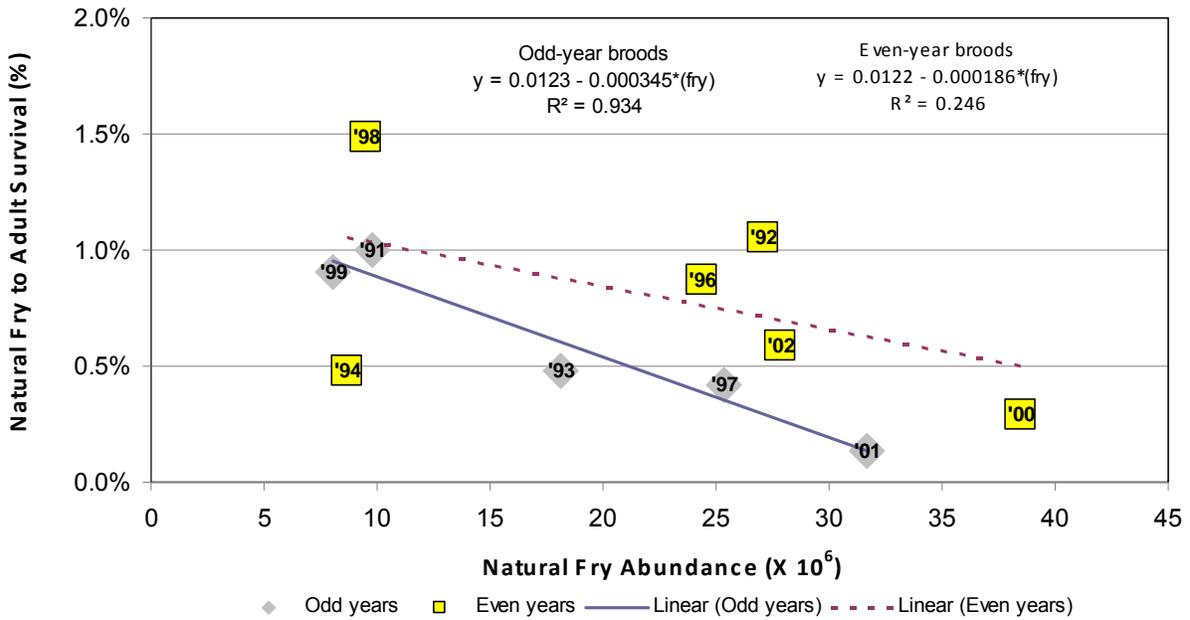


Figure 17—Estimated fry to adult survival of Cedar River natural origin sockeye vs. natural fry abundance for brood years 1991-2002 (w/o 1995), odd-year and even-year data graphed separately.

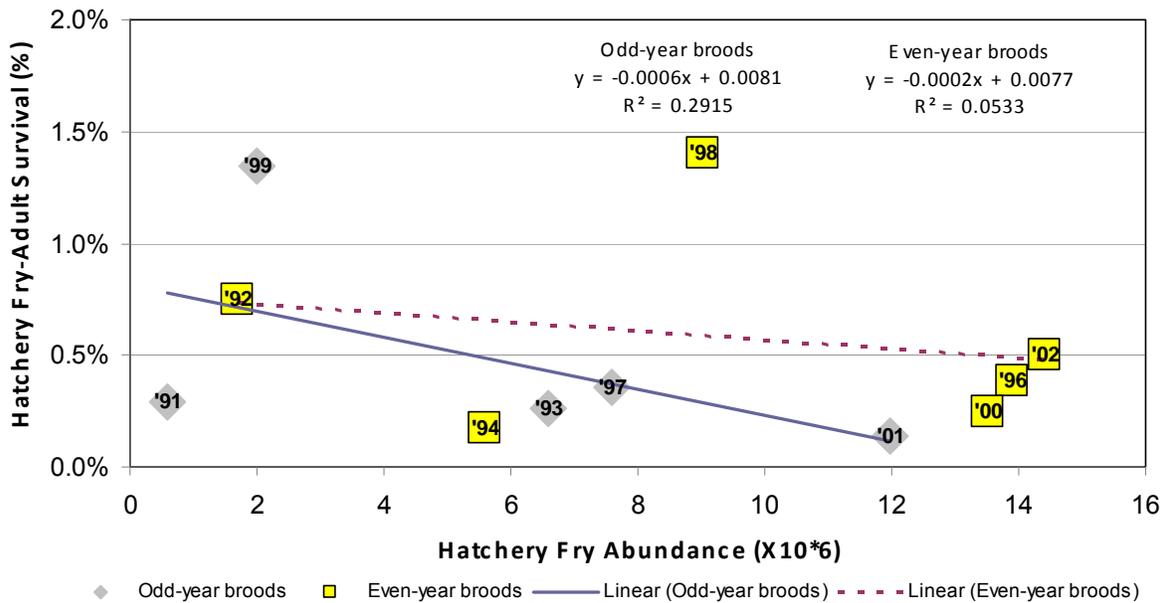


Figure 18—Hatchery-origin Cedar River sockeye fry to adult survival related to HOR fry abundance.

higher survival of even-year broods at a given fry abundance was evident. Again, density effects on both even- and odd-year brood datasets were indicated.

NOR fry-to-adult survivals were then plotted against the summed NOR + HOR fry abundances to determine if these data provided improved insight into the cause-effect relationships. A greater separation between the even- and odd-year brood datasets was observed (Figure 19), except that the 1994 data point remained at variance with the remaining five even-year broods.

Our conclusion based on these analyses was that while inadequate data exists for any dataset, the common pattern of higher fry-to-adult survival in even-year broods for both NOR and HOR fry strongly suggests that differential fry-to-adult survival on even- vs. odd-year broods is the cause of the differences observed between even- and odd-year recruitment dynamics in the S-R analyses. The density-dependent survival of NOR fry suggests that early survival may be a major bottleneck to the carrying capacity of Lake Washington for sockeye salmon. Even- and odd-year broods may be affected differentially leading to the above observation of differences between them in terms of optimal escapement.

Composite survival calculation

Using the measured survival rates at life stages, we calculated the average recruitment/spawner for the Cedar River NOR fish in the recent past. At 50% females and a mean fecundity of 3,334 eggs, the average egg to fry survival (13.5%) would yield 450 fry/spawning pair. Fry to presmolt survival of 2.91% reduces the number of juveniles/pair to 13.1 fish. Then applying the observed presmolt to adult survival rate (12.0%) yields approximately 1.6 recruits from each pair of spawning fish or 0.8 fish per spawner. In southern British Columbia sockeye stocks, recruitment of approximately 3-4 fish per spawner is considered average. Given that the egg-to-fry and the estimated presmolt to adult survival rates are within normal ranges for the geographical region, low fry to presmolt survival is the most likely source of the low productivity of Cedar River sockeye. Escapements of Cedar River sockeye in the past have often been greater than the above estimated \hat{S}_{MSY} points and many have yielded high fry abundances and low fry to presmolt survival which appear to produce low recruitment rates in these populations.

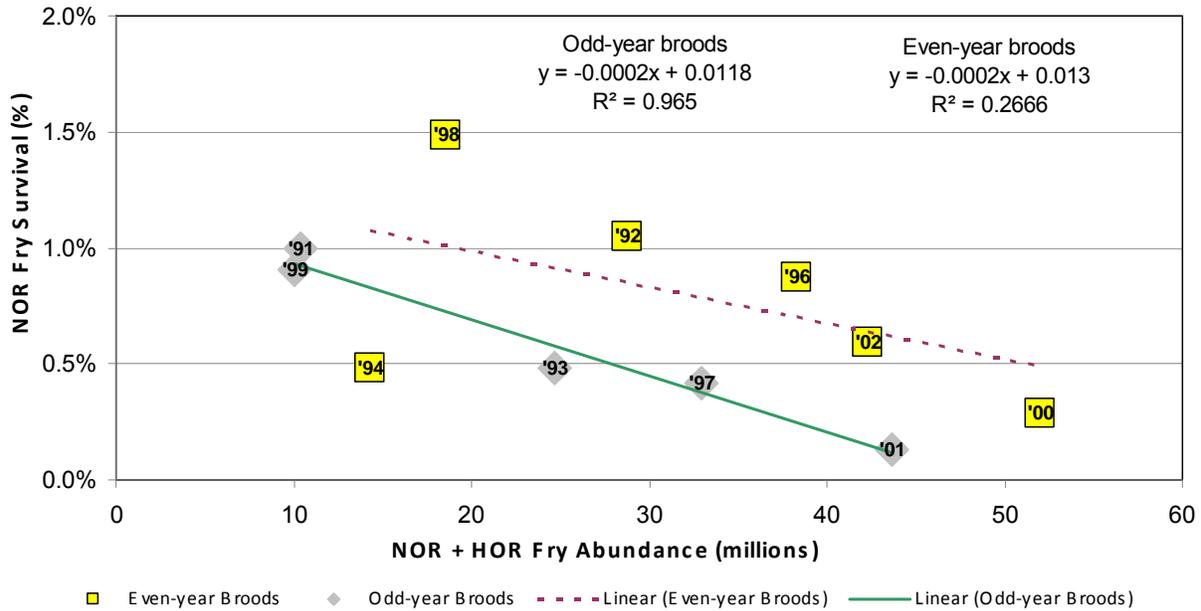


Figure 19—Natural origin sockeye fry survival to adults vs. NOR plus HOR fry abundance.

Hypotheses for mechanisms controlling Lake Washington sockeye productivity

Initially, we wish to acknowledge that the following analyses and conclusions require further study before being accepted and acted upon. However, we herein attempt to point out significant clues and to construct hypotheses for further study and testing. Extensive data collection efforts in the past provides a wealth of information that should be utilized to systematically analyze the issues raised in our observations of low in-lake survival and consequent low productivity of the Cedar River and other Lake Washington sockeye populations and to determine the causes of the even- vs. odd-year brood differences.

Thermal regime and fry emergence timing

Due to the relatively warm climate of the Cedar River watershed situated as it is in the lowlands of central Puget Sound, water temperatures generally remain well above freezing overwinter, promoting ongoing embryonic and alevin development (February mean temperature = 6.2°C; Kiyohara and Volkhardt 2008). The resultant emergence timing of natural fry tends to be quite early for sockeye stocks (median date = March 22). Hatchery fry are buttoned up and released nearly a month earlier (median date = February 27). Thus, fry entry into Lake Washington often takes place before or early in

the spring bloom period, potentially placing the fry at risk due to suboptimal food resources for large populations entering in the south end of the lake from Cedar River. Beauchamp et al. (2004) noted severe depletion of *Cyclops*, the preferred zooplankton food item in the guts of fry, between late February-early March, 2001 (mean = >30/L) and mid March-early April (mean = <5/L) in the southern portion of Lake Washington before rebounding in mid April and May, the traditional spring bloom period. Other zooplankton, including, *Daphnia*, *Diaptomus* and *Epischura* were in constant low abundance during the late winter-early spring. They also noted that sockeye fry consumed only *Cyclops* over 0.8 mm, which may have further limited foraging opportunities within the early lake entry period.

Average survival to maturity of hatchery fry that enter Lake Washington approximately one month prior to the NOR sockeye fry is estimated to be 0.53% vs. the average NOR fry to adult survival of 0.70% (both w/o the 1995 brood). The earlier lake entry timing of hatchery fry possibly places them at a greater disadvantage due to the longer period of lake residence prior to the spring bloom increases in the zooplankton food resources of the lake.

Examination of zooplankton data collected in systematic surveys over the years should provide information on the temporal patterns of zooplankton availability in southern Lake Washington during winter and early spring and suggest whether or not the depletion of zooplankton occurs consistently, and if this is a recent phenomenon.

Food competition factors

Depletion of food resources in the south end of Lake Washington during late winter and early spring may occur regularly due to a combination of foraging by sockeye fry and foraging by longfin smelt and stickleback that accumulate in that portion of the lake in winter months (see Figure 2 in Overman and Beauchamp 2006; Beauchamp pers. comm.). Woodey (1972) noted a shift of presmolt sockeye from the northern lake areas toward the middle and south end of the lake in winter months. He postulated that deep return water circulation in the lake driven by prevailing southerly winds that pile up water in the north end of the lake during fall-winter may passively displace deep dwelling fish in a southerly direction leading to an accumulation in the south end of the lake during winter. Foraging by the accumulated limnetic fish may result in low zooplankton resources for sockeye fry entering the lake from the Cedar River.

In addition, foraging by maturing (age 2) longfin smelt that spawn in the Cedar River in late winter (February-March; Moulton 1970) may exacerbate food competition.

Neomysis also feed on zooplankton (particularly *Daphnia*) and may compete with fish during the fall-winter months. Cycling in this population associated with predation by longfin smelt may be involved in crustacean zooplankton abundance regulation.

Cycling and abundance of longfin smelt

Longfin smelt in Lake Washington mature in late winter-early spring (February-March) as age 2 fish and show a strong cyclical pattern of abundance (Table 11) with large even-year broods and an order of magnitude smaller odd-year broods (Overman et al. 2006). Being age 2 fish at maturity, two year classes of smelt are found in the lake from summer, after larvae recruit to the limnetic zone, through mid-late winter when adults mature and spawn. While a cyclical pattern of smelt numbers existed in the mid to late 1960s (Moulton 1970), the abundance of smelt has increased substantially in the thirty to forty-year period between then and the early-mid 2000s while the sockeye abundance has declined.

Woodey (1972) reported 3-m Isaak-Kidd midwater trawl catches in October, 1968-1970 surveys, were composed, on average, of 79.6% sockeye and 12.2% age 0 plus age 1 smelt. Overman et al. (2006) and Overman and Beauchamp (2006, 2007) report hydroacoustic estimates in October, 2001-2006, indicating that juvenile sockeye now constitute an average of 3.9% of the limnetic fish, while the two year classes of smelt combined contribute 81.4%. Hydroacoustic estimates of presmolt sockeye in March surveys declined from averages of 4.8×10^6 for 1967-1969 broods to 3.1×10^6 for 1970-1981 broods, to 1.9×10^6 for 1982-1988 broods to 1.6×10^6 for 1991-1994 and 2000-2005 broods (see Ames 2006). However, the total lake population of limnetic fish increased by a factor of approximately 6.8X from 6.0 to 41.0×10^6 fish based on an extrapolation of the numbers and fraction of sockeye in the limnetic zone in the early years. Currently, an average of approximately 24×10^6 smelt reside in the lake (Table 11) versus approximately 1.2×10^6 in the late 1960s. We suggest that this large smelt population may sustain piscivorous fish during much of the year, possibly at higher abundances than in prior years.

Examination of long-term changes in the longfin smelt populations in Lake Washington using collections and hydroacoustic estimates may provide clues as to the timing of population changes leading to the current dominance of smelt in the limnetic fish population.

Table 11—Longfin smelt abundance and mean length in Lake Washington for the 2000-2006 brood years (Overman et al. 2006; Overman and Beauchamp 2006, 2007).

Brood year (yr)		October yr 0	March yr+1	October yr+1	March yr+2
2000	abundance	N/A	N/A	17.94 X 10 ⁶	0.14 X 10 ⁶
	mean length (mm)			94.0*	103.1*
2001	abundance	?	0.18 X 10 ⁶	1.94 X 10 ⁶	0.14 X 10 ⁶
	mean length (mm)		63.0*	121.2	120.0
2002	abundance	34.20 X 10 ⁶	9.91 X 10 ⁶	9.90 X 10 ⁶	0.83 X 10 ⁶
	mean length (mm)	52.2	73.1	99.3	97.6
2003	abundance	8.40 X 10 ⁶	0.67 X 10 ⁶	0.48 X 10 ⁶	1.54 X 10 ⁶
	mean length (mm)	49.6	68.1	122.2	101.0
2004	abundance	28.01X 10 ⁶	20.18 X 10 ⁶	10.11 X 10 ⁶	1.74 X 10 ⁶
	mean length (mm)	45.2	66.3	100.0	102.1
2005	abundance	3.25 X 10 ⁶	0.05 X 10 ⁶	1.97 X 10 ⁶	1.33 X 10 ⁶
	mean length (mm)	54.8	70.0	123.4	98.9
2006	abundance	28.74 X 10 ⁶	14.26 X 10 ⁶	N/A	N/A
	mean length (mm)	44.9	65.4		

* Rope trawl

Growth of juvenile smelt and sockeye

Growth of juvenile smelt on the large even-year cycle line show the negative effects of density (Table 11, Figure 20). This response seems to be most evident in the October trawl samples when even-year cycle age 1 smelt are present. We suspect that the cause may be depletion of the preferred food item of larger smelt, i.e., *Neomysis*, when smelt are abundant. However, it is clear that the size at which smelt are able to consume *Neomysis* is not reached by age 0 smelt in their first year in the lake (March mean length = 68 mm). Thus, juvenile smelt are likely to be feeding on a range of crustacean zooplankton species also utilized by sockeye in their first year. Competition between juvenile sockeye and age 0 smelt would likely take place after both species are recruited to the mid-lake areas, i.e., July through winter months.

Juvenile sockeye mean length data (Table 11) show a similar depression for odd-year brood sockeye growth on two years when even-year brood age 0 smelt were present in large numbers (Figure 21) and juvenile sockeye abundance was high (2001 and 2003 broods). The third odd-year sockeye brood (2005) had much better growth to October, 2006, samples but was a much smaller fry recruitment year. Even-year broods of juvenile sockeye reside in the lake when low abundances of odd-year brood age 0 smelt are present. Thus, the level of direct interspecific competition may be substantially reduced. The even-year broods of smelt are age 1 fish and may well have switched to foraging mainly on *Neomysis* and other larger prey rather than on smaller crustacean zooplankton species when the even-year brood juvenile sockeye are present, thus limiting the degree of interspecific competition. All three large even-year sockeye broods (2000, 2002 and 2004) grew well despite their high abundance, but when age 0 smelt were in low abundance (Table 11). Samples and data on the food partitioning within the limnetic zone of Lake Washington should be available to evaluate when and where interspecific competition is most intense, but the scope of this report does not extend to this examination.

Potential sockeye fry – mature smelt interaction

As discussed above, even-year brood sockeye fry which enter the lake in late winter and early spring of odd-numbered years, tend to have higher survival than odd-year broods (Figure 16), particularly when large fry populations enter the lake. While the density-dependent survival suggests intraspecific competition and high mortality, perhaps as a result of zooplankton depletion in years of high lake densities of other species, the spatial-temporal overlap of mature smelt and odd-year sockeye fry in Lake Washington at the mouth of the Cedar River raises the question as to whether predation by maturing smelt on sockeye fry may be involved.

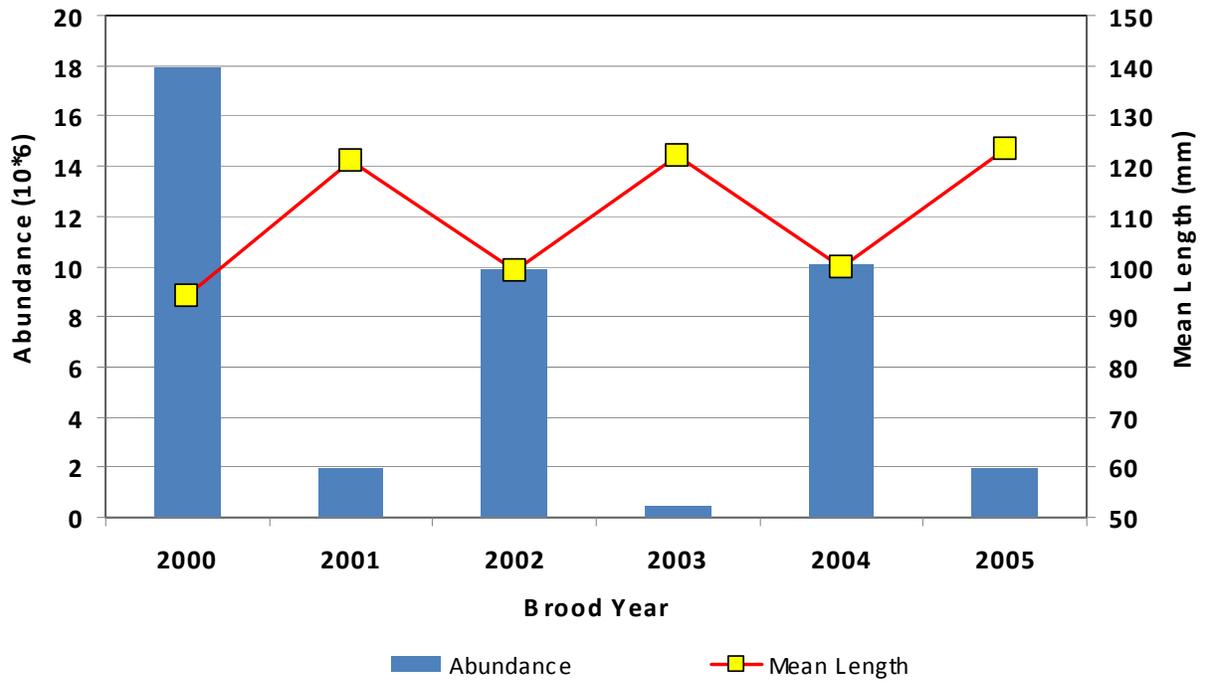


Figure 20—Abundance and mean length of age 1 longfin smelt in October.

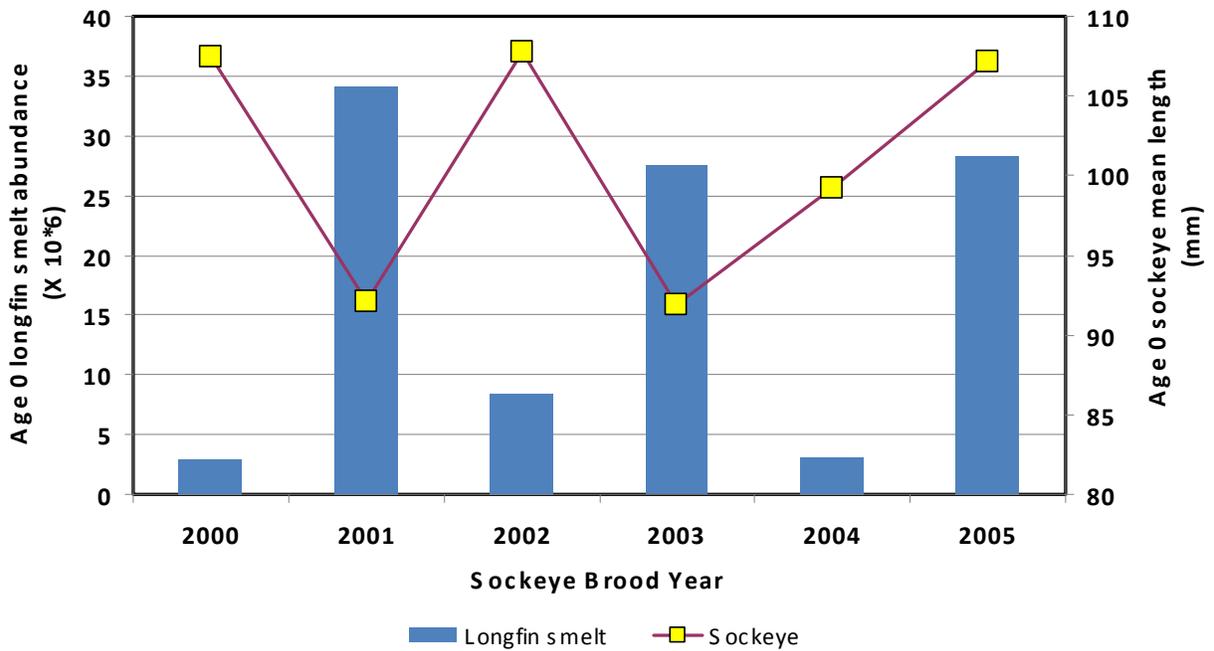


Figure 21—Lake Washington age 0 sockeye mean length vs. age 0 longfin smelt abundance estimates in October.

One mature smelt in the late 1960s was found with a sockeye fry in its gut, but since smelt are the main predator on *Neomysis*, which are by far the largest (up to 14mm in length) non-fish species in the limnetic zone, opportunistic foraging on sockeye fry near the Cedar River may take place when large even-year adult smelt prepare for river entry and spawning. No estimates of smelt abundance entering the Cedar River have been made, but we note that even-year brood smelt abundances in Lake Washington during October surveys has varied from 9.9 to 17.9 X 10⁶ fish in recent years (Table 11). We note, as well, that in March surveys, odd-year brood sockeye fry abundances have been lower than even-years broods in the 2001-2006 period (Table 10). Whether this suggests consumption or distributional changes to reduce predation risk cannot be discerned from the data.

Summary of hypothesis

The data on Lake Washington sockeye show a generally low productivity, with occasional high recruitment years. This overall pattern is evident from the late 1960s to late 1980s and much reduced numbers in recent years. These populations exist near the southern limit of the range of the species and juveniles interact with competitor and predator species not commonly encountered in more northern and less culturally impacted lake systems. Consequently, average survival rate may naturally be lower in Lake Washington sockeye populations than might be expected in other systems. However, we suspect that recent changes to fish populations in Lake Washington have led to lowered sockeye productivity, particularly for the odd-year broods.

The timing of emergence in Cedar River sockeye fry, the indications of depletion of zooplankton in the southern portion of Lake Washington in winter months associated with the accumulation of limnetic fish, the density dependent growth relationships with smelt abundance and the overall low sockeye fry to presmolt survival estimates appear to be related. To this we add our observations of differential survival in even-year and odd-year broods of sockeye.

We hypothesize that the low survival of sockeye fry entering Lake Washington from the Cedar River in winter/early spring is the result of intertwined mechanisms: (a) intraspecific competition during early lake residence in the sockeye fry population after preferred zooplankton species have been depleted by the foraging of abundant limnetic smelt and other species that are passively displaced into the southern half of the lake during fall-winter, (b) interspecific competition, particularly between odd-year brood age 0 sockeye and large populations of even-year brood age 0 longfin smelt that appear to affect sockeye growth in years when sockeye fry abundance is high, (c) high predation rates by piscivores that are usually supported by large longfin smelt populations.

Actual mortality during lake residence is likely due to predation by larger piscivorous fishes (cutthroat trout and other species) and birds, and may be more intense when odd-year brood juvenile sockeye grow more slowly. Also, odd-year brood sockeye fry may have increased vulnerability to predation during the early months of lake residence due to the low abundance of limnetic fish species following maturity and spawning of even-year brood smelt. Low abundance of age 1 odd-year smelt may leave the predators seeking alternate food sources, thus leading to higher predation rates on sockeye. (This may also be the mechanism leading to smelt population cycling.) Thus, the potential exists for differential mortality of odd- and even-year broods of sockeye dependent on juvenile growth patterns relative to longfin smelt abundance and relative vulnerability of sockeye when smelt are scarce. That the greatest difference between odd- and even-year brood survival appears to occur when fry abundances are highest suggests that the food depletion is most severe when odd-year brood sockeye enter the lake.

In our examination of the data, we considered the possibility that predation by large piscivorous fishes and birds may be driving the variable survival of even- vs. odd-year brood juvenile sockeye. While predators undoubtedly consume the juvenile sockeye lost in the lake, we suggest that the increase in the cyclical abundance of longfin smelt is the most important factor in the recent decline of productivity of the odd-year sockeye populations. The large populations of even-year brood smelt likely support the predator populations. When smelt are in low abundance in the period between the spawning of even-year smelt in late winter and the recruitment of their offspring in midsummer, sockeye may be particularly vulnerable. Thus, we suggest that the survival of odd-year brood juvenile sockeye in Lake Washington is currently being driven by the cycling of longfin smelt abundance in one, or more, of the following means: (1) through the consumption of newly recruited sockeye fry in the southern end of Lake Washington by adult longfin smelt, (2) through increased predation rates during low smelt abundance subsequent to the maturation and spawning of even-year broods of smelt, and (3) through negative growth effects due to competitive interaction between juvenile sockeye and age 0 even-year brood smelt.

Estimated optimum fry abundance

We used the relationships between even- and odd-year brood Cedar River NOR fry to adult survival vs. fry abundance to determine if these relationships could provide insight into the optimum escapement level for the population. Even- and odd-year brood NOR fry regressions (Figure 17) were used to predict the adult abundance response at variable fry inputs for the two cases. A linear regression forced through the origin and fit to the 1991-2007 brood Cedar River NOR fry vs. adult spawner data provided a “replacement line” for use in estimating the number of adult spawners

required to produce a given number of fry. Subtraction of the replacement line value, as in the Ricker S-R analysis, provided estimates of yield at given fry abundance levels.

Maximum Cedar River NOR adult recruitment estimated via this model (equivalent to S_{max}) occurred at approximately 18×10^6 fry for odd-year broods and $30\text{--}35 \times 10^6$ fry for even-year broods (Figure 22). These levels of fry would equate to escapements of approximately 77,000 adult spawners for odd-year broods and 130,000 to 150,000 spawners for even-years broods. The MSY points occurred at 12×10^6 fry and 21×10^6 fry, for the odd- and even-year Cedar River NOR sockeye broods, respectively. These levels of fry recruitment equate to escapements of approximately 51,000 adult spawners for odd-year broods and 90,000 spawners for even-years broods. Given that Cedar River NOR sockeye comprise approximately 84.5% of the total NOR spawners in the Lake Washington system, the optimum escapement estimates for Cedar River NOR sockeye would be increased by a factor (i.e., 1.18X) to approximately 60,000 spawners on odd-years and 107,000 spawners on even-years, respectively, for the natural spawning populations in the entire watershed.

S-R analyses of 1982-2002 even- and odd-year broods was conducted for all Lake Washington NOR sockeye and indicated that the 1983-2001 odd-year brood data produced \hat{S}_{MSY} escapement estimates of 60,000 and 69,500 spawners, depending on the assumption as to which values to use for “recruits” and 1982-2002 even-year brood data produced a \hat{S}_{MSY} escapements of 130,000 and 146,000 spawners in the entire lake. The MSY escapements estimated from the limited fry-adult survival data (adjusted to reflect all Lake Washington sockeye) and from the S-R analysis and appear to be close for odd-year broods (60,000 vs. 60,000 or 69,500 spawners), but for even-year broods, MSY values differ somewhat (107,000 vs. 130,000 or 146,000 spawners). The reason for the different outcomes may be associated with the use of a linear fit of the regression of fry recruitment vs. adult spawners to obtain a “replacement” line. Additional work is required to determine the best relationship to use. However, the MSY values obtained in this optimization exercise mimic the outcome of S-R analyses which showed relatively low optimal abundances of spawners and support the S-R analyses that show large differences between even- and odd-year brood sockeye.

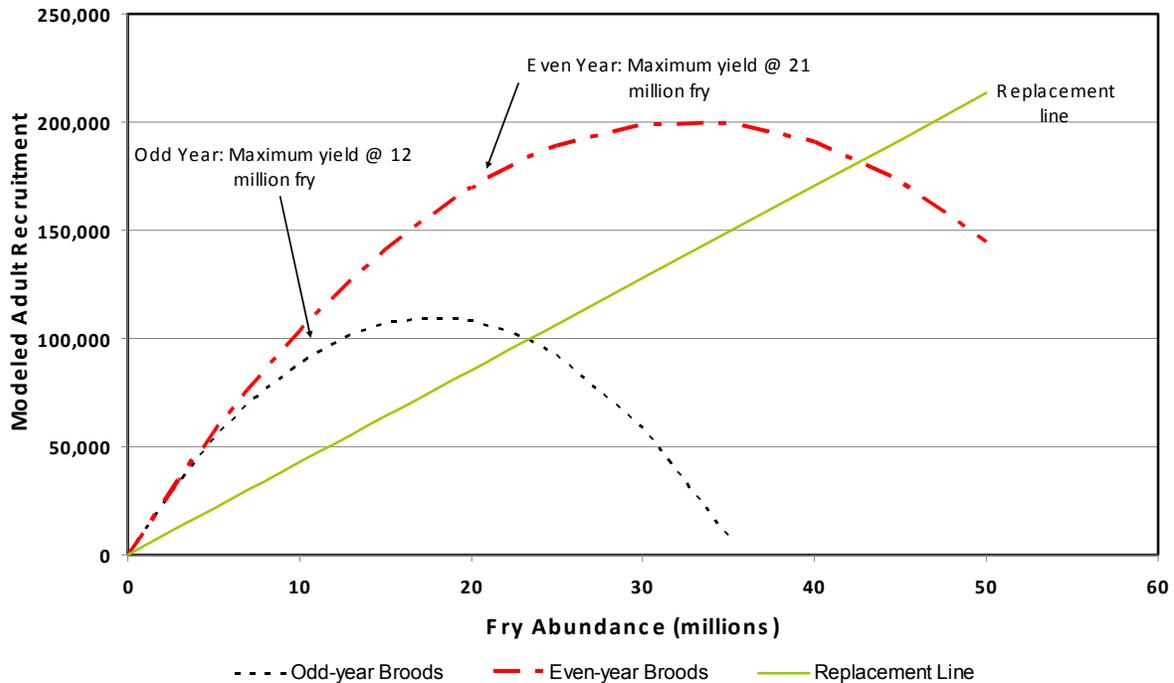


Figure 22— Model of Cedar River sockeye NOR adult recruitment using fry to adult survival vs. fry abundance relationships for even-year and odd-year broods fit by linear regressions, for brood years 1991 to 2002.

Examination of Ballard Lock counts in relation to catch and escapement

Beginning in the early 1990s, the relationship between Ballard Lock counts and accounted fish in spawning escapement plus in-lake catch deteriorated and became a major concern because of the critical use of Lock count in the management of the stocks. Potential causes for the observed lower numbers of fish accounted in the escapement and catch are: (1) en route mortality in the Ship Canal and Lake, (2) changes to the distribution of spawning in the Cedar River causing underestimates of abundance, and (3) recycling/recounting of fish at the Locks. Newell et al. (2007) found evidence of mortality in 2004 associated with high water temperatures in the Ship Canal. Other recent years of high water temperature have also shown evidence of en route losses. Ames (2006) discusses the potential for spawner distributional changes in the Cedar River and speculates that assumptions in the traditional AUC method of escapement estimation have been violated but could not quantify the impact on escapement estimates. Herein we briefly examine (3), the potential for recycling/recounting at the Locks.

Pacific Salmon Commission gillnet test fishing operations in Canadian Area 20 (western Juan de Fuca Strait) catch small numbers of Lake Washington sockeye along with Fraser River fish. We related cumulative seasonal Lake Washington sockeye

CPUE in the test fishery to Ballard Lock-based estimates seven days later as: Sum Lock count/Area 20 CPUE for overlapping time periods each year. We examined these annual “efficiency” factors in relation to the ratio of spawning escapements plus catch vs. Lock count. The Area 20 dataset limited our analysis to 1998-2006 migrations. The regression between test fishing efficiency and the ratio of accounted fish to Lock-based estimates was negative, suggesting that in years when the Lock count:CPUE ratio was high, the difference between cumulative Lock counts and accounted fish in escapement and catch was also large. The three highest count:CPUE data points were three of the four lowest percent accounted in the lake. However, the fit of the regression was poor: $r^2 = 0.24$, $n=9$. Data are insufficient to conclude that recycling or error in the Lock counts are the cause of the discrepancy, but the data suggest that a more thorough analysis be conducted.

Water temperature data were inadequate to assess environmental impacts on the potential for recycling of fish at the Locks.

Sources of error

The above analysis made use of data provided by WDF&W from the collections of individual program datasets. We have used these data as faithfully as possible. However, errors may have been included inadvertently. Minor data differences will not have material effect on the conclusions.

Use of short time series datasets, particularly the fry abundance and recruitment from those fry estimates in brood years, 1991-2002, may pose a risk, both from the small number of observations we could use ($n = 11$), but also from possible atypical recruitment in this particular time period. While the S-R recruitment data for 1991-2002 brood years were not at variance with the remainder of the 1982-2002 time series of data used in the primary S-R analysis (Figure 4), the shift in recruitment dynamics from the 1967-1981 brood years to the 1982-2002 period raises questions as to the comparability of the data. Future shifts in environmental conditions within the Lake Washington watershed or in ocean conditions that affect post-lake survival may invalidate conclusions drawn from the most recent data.

We used Ricker’s model to estimate stock-recruitment parameters. We could find no obvious reason not to use this model for the primary data set of 1982-2002 for Cedar River and Lake Washington. It is a model widely used by management jurisdictions for sockeye and other salmon species to provide benchmarks for management. The Beverton-Holt model was tested and resulted in estimates of S_{MSY} that were 30-40% lower than those from a log-normal Ricker model. We could not address measurement error within the framework of this analysis; incorporation of measurement error in

estimating spawners or recruits may lower or raise the estimates of S_{MSY} presented herein.

The lack of age composition data from the non-Cedar stocks in many years has introduced some bias into the analysis, as evidenced by the age proportions differences between Bear/Cottage Creek samples and Cedar River samples in 1998-2000:

Bear/Cottage	Age 3	Age 4	Age 5
1998	0%	93%	7%
1999	0%	68%	32%
2000	0%	82%	18%
Cedar NOR			
1998	0%	63%	37%
1999	0%	20%	80%
2000	0%	94%	6%

For this reason we omitted any spawner-recruit analysis of the non-Cedar River stocks in this document. The run statistics for these stocks are in Appendix 1.

The lack of age composition data from the non-Cedar stocks will not have a significant effect on analysis of the Lake Washington composite data as it is dominated by Cedar River, for which there is extensive age data for in recent years. Age composition data from some of the early years in the data set were taken from differing gear and location and sample sizes were relatively low (< 400 fish).

Based on our observations of the 1995 brood recruitment data, Cedar River age analyses may require a systematic re-examination to ensure that errors are detected and corrected. Also, a proportion of Lake Washington sockeye smolt in summer (June-July) of their first year (age 0 smolts) and mature as age 0.1, 0.2 and 0.3 fish. These fish are not recognized in the dataset and may constitute a systematic error in the assignment of recruits to proper brood. A full review of these datasets are required, however, in our opinion, the effect of this systematic error on our S-R analyses should be minimal.

Conclusions

- 1) There has been a decrease in the adult production and productivity of sockeye salmon from the Cedar River subsequent to the 1967-1981 brood years; and for all Lake Washington sockeye stocks for returns from odd-year brood years after 1981.
- 2) There does not appear to be a drop-off in production at lower spawning levels that would extirpate the stock, i.e., no depensatory limb.
- 3) No measurement error analysis of the stock-recruit data could be undertaken because estimates of precision for escapements and harvest do not exist.
- 4) We conclude that the full (1968-2002) even-year brood dataset provides the best estimates of \hat{S}_{MSY} , at approximately 150,000 spawners, based on the Lake Washington counted escapement vs. Lock-recruit dataset (Table 6 Case 2 and Table 7). Odd-year brood data for 1983-2001 must be considered preferable for future management of odd-year broods.
- 5) Management can continue to utilize the Lock counts as a trigger for fisheries, but an escapement goal determined from the above data needs a cushion in the Lock counts because the accounting of freshwater harvests and escapements, on average, account for 73% of the Lock count from 1992-2007.
- 6) Management should take into account hatchery production and its effect, if any, on natural fry production. Since those hatchery-produced fish which are not taken for brood stock are spawning in Cedar River, management could be as simple as a Lock count of the escapement goal + brood stock + a cushion for fish not accounted for after passing the locks.
- 7) Comparison of Cedar River sockeye with a suite of reference stocks indicates that the Cedar River Ricker "a" productivity parameter is the lowest observed within those stocks.
- 8) Harvest rate at MSY for Cedar River sockeye (30%) was lower than all reference stocks which showed a geometric mean HR of 74%. Recruitment densities per unit lake area at MSY also showed much lower density for Cedar River sockeye compared to the eight reference stocks.
- 9) Cedar River egg to fry survival estimates averaged 13.5% which is comparable to other sockeye stream incubation sites.

- 10) Examination of the juvenile sockeye database indicated that natural fry abundance was positively related to spawner abundance, positively related to high minimum flows during spawning and negatively related to maximum flow during spawning.
- 11) Estimated in-lake survival from fry entry to presmolts the following spring for 2000-2005 brood years was approximately 2.91%, a very low survival rate for this life history stage.
- 12) Presmolt to adult survival in three recent years approximates the earlier average survival estimate of 12.0%.
- 13) Survival of Cedar River NOR fry to maturity was negatively related to Cedar River natural fry abundance. In addition, even-year broods survived at rates substantially higher than odd-year broods at comparable fry input levels.
- 14) A model of adult recruitment based on observed Cedar River NOR fry survival data for odd- and even-year broods showed a optimal level of 12 and 21 million NOR fry, respectively, compared to the recorded immigration to the lake of up to 38.7 million NOR fry. This finding supported S-R analyses and suggests that a bottleneck exists in the survival of fry, thus limiting the optimal fry abundance.
- 15) Density-dependent survival of fry in Lake Washington is associated with early arrival of large numbers of fry prior to the spring bloom of zooplankton suggesting intraspecific competition during early lake residence. Interspecific competition with other limnetic species, in particular, with large even-year broods of longfin smelt limit odd-year brood sockeye as evidenced by lower growth and survival.
- 16) We hypothesize that abundant even-year brood longfin smelt negatively impact sockeye survival by one or more of the following interactions: (1) through the consumption of newly recruited sockeye fry in the southern end of Lake Washington by adult longfin smelt, (2) through increased predation rates by piscivores during low smelt abundance subsequent to the maturation and spawning of even-year broods of smelt, and (3) through negative effects of slower growth due to competitive interaction between juvenile sockeye and age 0 even-year brood smelt.

Recommendations

- 1) We recommend that the decline in productivity of odd-year brood Cedar River sockeye be investigated since even-year broods Cedar River and non-Cedar sockeye do not show a similar decline.
- 2) We recommend that additional study of available data be conducted to develop a working hypothesis regarding the interaction between juvenile sockeye and other limnetic species in Lake Washington and to define studies that would elucidate cause-effect relationships to better understand and manage the sockeye resource.
- 3) We recommend systematic field studies of Cedar River sockeye fry abundance and growth in southern Lake Washington during the spring to early summer period related to zooplankton abundance and to the abundance and feeding patterns of longfin smelt, stickleback and other species.
- 4) We recommend that total escapement in the Cedar River be estimated by a means independent of the AUC method used presently to determine the accuracy of the AUC method.
- 5) Management of the resource must consider the abundance and timing of hatchery fry recruitment. Delayed release of hatchery fry may provide much improved survival of HOR fry rather than possibly introducing a negative impact on natural fry.

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Appendix Table 1—Estimated harvest, escapement and annual run size of sockeye salmon from non-Cedar River stocks in Lake Washington, 1967-2007.

Calendar year	Total harvest	Escapement	Total annual run
1967	590	18,250	18,840
1968	2,217	12,000	14,217
1969	6,734	20,000	26,734
1970	1,122	14,000	15,122
1971	37,630	18,838	56,468
1972	5,046	22,586	27,632
1973	14,619	15,710	30,329
1974	2,365	11,447	13,812
1975	2,298	5,705	8,003
1976	1,966	20,260	22,226
1977	13,812	25,700	39,512
1978	543	26,850	27,393
1979	1,075	33,500	34,575
1980	12,478	12,922	25,400
1981	628	15,908	16,536
1982	2,736	36,116	38,852
1983	5,015	36,333	41,348
1984	10,472	35,565	46,037
1985	701	29,390	30,091
1986	842	33,928	34,770
1987	1,724	26,864	28,588
1988	24,474	18,806	43,280
1989	570	4,972	5,542
1990	476	17,825	18,301
1991	365	11,267	11,632
1992	265	59,659	59,924
1993	173	18,539	18,712
1994	698	51,125	51,823
1995	79	4,196	4,275
1996	13,926	75,621	89,547
1997	231	11,126	11,357
1998	354	11,114	11,468
1999	94	2,280	2,374
2000	12,475	82,090	94,565
2001	559	14,930	15,489
2002	6,536	56,700	63,236
2003	384	3,365	3,749
2004	5,396	16,064	21,460
2005	43	5,824	5,867
2006	11,275	26,727	38,002
2007	133	4,549	4,681
Averages			
1967-2007	4,954	23,626	28,580
1967-1981	6,875	18,245	25,120
1982-2007	3,846	26,730	30,576