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Changes in the Distribution and Density of Pink, Chum, and Chinook Salmon Spawning in the Upper Skagit River in Response to Flow Management Measures

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Abstract.—We analyzed the abundance and spatial distribution of spawning pink salmon *Oncorhynchus gorbuscha*, chum salmon *O. keta*, and Chinook salmon *O. tshawytscha* in a 27-mi section of the upper Skagit River, Washington, regulated by the Skagit Hydroelectric Project. Densities of spawning salmon were compared among three contiguous reaches of the upper Skagit River before and after the implementation of flow management measures in 1981. The measures were intended to minimize redd dewatering during the spawning and incubation periods and fry stranding during the emergence and outmigration periods. Field monitoring confirmed that increasing the minimum incubation flows created improvements in redd protection levels. Greater protection of fry from stranding was achieved by substantially reducing the annual number of downramping events and by reducing downramping during daytime, when fry are most vulnerable to stranding. Spawner abundance of all three species progressively increased in an upstream direction following implementation of flow measures; increases were greatest in the reach immediately below the hydroelectric project. The upstream shift in spawner abundance was highly significant based on factorial analyses of variance. The greatest increases in spawner abundance for Chinook salmon and chum salmon were observed during even years, when pink salmon did not spawn. Mean spawner abundance in the upstream-most study reach increased from 311 to 1,169 carcasses/mi (odd years) for pink salmon, from 6 to 115 fish/mi (odd years) or 58 to 462 fish/mi (even years) for chum salmon, and from 48 to 49 redds/mi (odd years) or 59 to 65 redds/mi (even years) for Chinook salmon. The total number of pink salmon and chum salmon spawners significantly increased within the study area after 1981. These increases were substantially greater than those observed concurrently in other areas of the Skagit River basin and in other northern Puget Sound rivers. The average number of Chinook salmon spawners remained unchanged in the study area after 1981, while substantially declining in other unregulated Skagit River subbasins and most Puget Sound rivers. The study area now possesses the greatest percentage of pink, chum, and Chinook salmon spawners within the Skagit River basin. The Skagit River presently supports the largest run of native Chinook salmon in the Puget Sound region and the largest runs of pink and chum salmon in the coterminous United States.

Streamflow alteration is one of many types of habitat disturbance contributing to the decline of salmon populations in the Pacific Northwest. Numerous studies have examined the short-term impacts of water resource projects on Pacific salmon *Oncorhynchus* spp. and their habitat (Hamilton 1976; Stober 1980; Woodin 1984; Pflug 1989). These studies, when combined with the results of habitat modeling efforts (e.g., instream flow studies), are being used to prescribe habitat measures to protect and restore fish populations. The development and implementation of habitat protection and restoration measures for salmon species and steelhead *O. mykiss* will dramatically increase in the near future due to recent and upcoming listings under the Endangered Species Act (ESA). Unfortunately, there is very little information on the long-term effectiveness of flow-based habitat protection measures, including flow management of rivers below dams, on salmon abundance.

The Skagit River, Washington, possesses the largest run of Chinook salmon *O. tshawytscha* in the Puget Sound region, the largest runs of pink salmon *O. gorbuscha* and chum salmon *O. keta* in the coterminous United States and regionally large runs of coho salmon *O. kisutch* (WDFW et al. 1994). The Skagit Hydroelectric Project is located on the upper Skagit River and consists of three hydroelectric dams, two regulating reservoirs, and a large storage reservoir (Figure 1). The operation of these facilities greatly affects the flow regime of a 27-mi section of the upper Skagit River between the town of Newhalem and the confluence of the Sauk River. As a result of Skagit Hydroelectric Project operations, flows were altered, especially during the spring and early summer, com-

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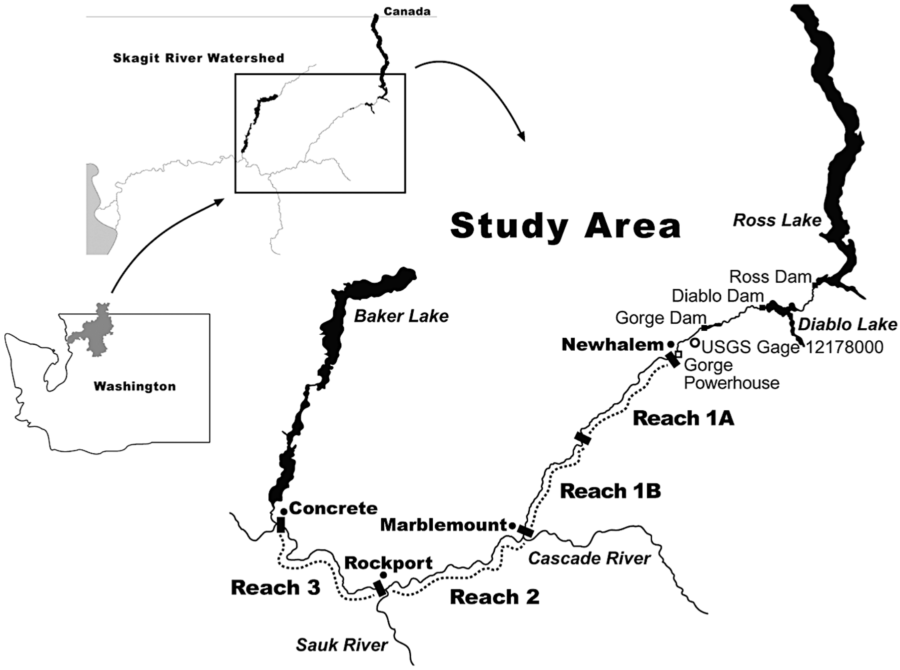

FIGURE 1.—Map of the Skagit River basin, Washington, where the effects of flow management measures on salmonids spawning below the Skagit Hydroelectric Project were studied. The 27-mi study area extended from the Gorge Powerhouse to the Baker River confluence.

pared with those occurring under natural (predevelopment) conditions (Graybill et al. 1979). Further, large hourly and daily flow fluctuations resulted from power generation cycling, which followed power demand by the City of Seattle.

A number of studies were conducted during the 1970s and 1980s to investigate the impacts of flow alterations on salmon in the upper Skagit River. These included studies of the effects of flows on the periodicity and spatial distribution of spawners, spawning habitat area, embryonic development and incubation timing, and survival of eggs and alevins under various conditions of dewatering (Graybill et al. 1979; Stober et al. 1982). The effects of flow fluctuations on salmon and steelhead spawning behavior, redd selection, alevin and fry behavior during dewatering, and fry stranding mortality on gravel bars were also studied (Thompson 1970; Graybill et al. 1979; Stober et al. 1982; Woodin 1984; Monk 1989; Pflug and Mobrand 1989). These studies found that the upper Skagit River provides some of the most important salmon and steelhead spawning habitat in the Skagit River basin. However, because the upper river was subject to frequent flow changes caused by project operations, egg and embryo mortality reached high levels, especially during the posthatch, preemergence period (Stober et al. 1982). Diel reductions in flow (downramping) resulted in periodically high levels of fry stranding on gravel bars and in potholes. Pflug (1989) found that salmon fry were most susceptible to stranding during daylight hours at all tested downramp rates. Salmon fry stranding rates increased seven- to eightfold when downramping occurred during the day instead of at night (Pflug 1989).

As part of Skagit Hydroelectric Project relicensing by the Federal Energy Regulatory Commission (FERC), Seattle City Light (a publicly owned utility of the City of Seattle) negotiated interim and final agreements with state and federal resource agencies and tribes, resulting in a number of major changes to project operations (Table 1). These changes were intended to reduce the aforementioned negative impacts of project-related flow changes on salmon and steelhead. Interim flow measures were effective during 1981–1990 prior to FERC relicensing, in an effort to increase the level of fish protection while additional studies were conducted. The measures were intended to protect incubating eggs and embryos of pink, chum, and Chinook salmon and steelhead from dewatering and to minimize the stranding of salmonid fry on gravel bars. Once the additional stud-

TABLE 1.—Progression of operational changes at Skagit Hydroelectric Project resulting from the pre-agreement to the interim and final agreements negotiated during Federal Energy Regulatory Commission relicensing. The term ''downramp'' refers to a flow reduction; cfs = cubic feet/s.

Conditions	Spawning flow range (cfs)	Minimum flow release (cfs)	Downramp amplitude limit (cfs)[a]	Maximum downramp rate (cfs/h)	Daytime downramping	Best-effort agreement[b]
Pre-agreement	No limit	1.000	None	No limit	Allowed	No
Interim agreement	4,200–7,000	1,000–2,300	None	4,000	Allowed	No
Final agreement	2,500–5,000	1,500–2,600	4,000	3,000	Not allowed[c]	Yes

[a] Difference between the highest and lowest flow releases during any 24-h period due to a flow reduction.
[b] Commitment to voluntarily surpass the required protection measures if conditions allow.
[c] Not allowed unless operational flow releases exceed an established threshold.

ies were completed, a more comprehensive and science-based set of flow measures were implemented in January 1990 as part of the final fisheries settlement agreement. To provide eggs and embryos with greater protection from dewatering, the final measures imposed more stringent constraints on maximum flows during spawning and higher minimum flows during incubation. These changes substantially reduced the difference between spawning and incubation flows, thereby reducing the area of the river channel subjected to dewatering. Fry stranding prevention was implemented by limiting project-induced downramping to nighttime hours, by further limiting the downramp rates, and by limiting the amplitude of flow fluctuations.

Noticeable shifts in the abundance and distribution of pink, chum, and Chinook salmon spawners were observed in the upper Skagit River during the 1980s through the mid-1990s (WDFW et al. 1994; Hard et al. 1996). Significant increases in total escapement of pink salmon (Hard et al. 1996) and chum salmon (Johnson et al. 1997) were also observed during this period. Chinook salmon escapement remained stable while seriously declining in other basins in the Puget Sound region, to the point that the stock was listed as threatened under the ESA (NMFS 1999).

We sought to determine whether the observed changes in abundance and distribution of pink, chum and Chinook salmon spawners in the upper Skagit River were statistically significant and whether these changes were attributable to the salmon protection measures implemented for the Skagit Hydroelectric Project. We analyzed salmon spawning data to determine how the abundance and longitudinal distribution of spawners changed after implementation of flow management measures in 1981. We also compared temporal escapement trends in the upper Skagit River with those of other Skagit River subbasins and other northern Puget Sound rivers to determine whether observed changes were unique to the study area. Finally, we analyzed possible relationships between temporal trends in flow characteristics and spawner abundance to determine if the observed changes in abundance could be linked to implementation of flow measures.

Study Area

The Skagit River originates in British Columbia and flows southward across the international border into Ross Lake, a 24-mi-long storage reservoir formed by Ross Dam at river mile (RM) 105 (Figure 1). The river then passes Diablo Reservoir and Dam and Gorge Reservoir and Dam. Gorge Dam (RM 97) is the lowermost dam on the main-stem Skagit River. The three facilities together constitute the Skagit Hydroelectric Project. Gorge Dam and Powerhouse are located at the upper end of the natural distribution of anadromous fish in the Skagit River, where increases in stream gradient and reduced channel width restrict further upstream migration (Smith and Anderson 1921). The river then flows westward for 94 mi until it enters Puget Sound near Mount Vernon, Washington. The 27 mi of the Skagit River below Gorge Powerhouse (located at Newhalem) is the reach most affected by the operation of the Skagit Hydroelectric Project (Graybill et al. 1979; Gislason 1980). The influence of this project on river flows decreases progressively downstream due to inflows from a number of tributaries, the largest being the Cascade River (RM 78.2), the Sauk River (RM 67), and the Baker River (RM 56.5). The mean annual flow of the Skagit River is 4,480 cubic feet per second (cfs) at Newhalem, 6,110 cfs near Marblemount (just above the confluence with the Cascade River), 15,090 cfs at Concrete (just below the confluence of the Baker River), and 16,660 cfs near Mount Vernon (Wiggins et al. 1997).

We studied the 27-mi section extending from

TABLE 2.—Life history stage timing for pink salmon, chum salmon, and Chinook salmon in the upper Skagit River, Washington (Stober et al. 1992; Meyers et al. 1998; Hard et al. 1996).

Species	Typical spawning age (years)	Spawning period[a]	Incubation period	Emergence period	Outmigration period
Pink salmon	2	Sep–Oct	Sep–Mar	Feb–Apr	Feb–Apr
Chum salmon	3 or 4	Nov–Dec	Nov–May	Mar–May	Mar–May
Chinook salmon	3 or 4	Aug–Oct	Aug–Apr	Jan–Apr	Jan–Aug

[a] Skagit River basin pink salmon spawn only in odd-numbered years.

Newhalem to the confluence of the Sauk River (Figure 1). This reach flows through a low-gradient (<0.2%), meandering floodplain in a narrow valley bounded by the steep topography of the Cascade Mountains. Although the dams have cut off the recruitment of gravel from the upper main stem, spawning-sized gravel is abundant in this section because of bed load contributions from tributaries and extensive glacial gravel deposits located along the floodplain. Substrates are dominated by small- and large-sized gravel and cobble located on extensive gravel bars.

The Skagit River and its tributaries have historically provided the most abundant runs of naturally spawning Chinook salmon in the Puget Sound region (WDFW et al. 1994; Meyers et al. 1998). The Skagit River basin currently supports a run of about 11,000 native summer–fall Chinook salmon, the largest in the Puget Sound region (WDFW 2003). Six genetically distinct runs of Chinook salmon presently exist in the Skagit River basin, including three spring runs, two summer runs, and one fall run (Meyers et al. 1998). Chinook salmon in the study area are dominated by a native, summer-run substock. Releases of hatchery-reared spring Chinook salmon downstream of the study area have little or no influence on the number of Chinook salmon observed within natural spawning grounds in the study area. Washington Department of Fish and Wildlife (WDFW) data collected annually from the spawning grounds have shown little evidence of hatchery stock straying (WDFW et al. 1994). Life history stage information for Chinook salmon from the study area is summarized in Table 2. Emergent fry in the study area exhibit an ocean-type life history, with most fry migrating to the ocean by the late spring or early summer (Meyers et al. 1998).

Pink salmon in the study area are of native origin. Pink salmon spawn during odd-numbered years throughout the Skagit River drainage in large numbers, with escapement levels over the last 25 years ranging from approximately 100,000 to 1.4 million spawners (WDFW 2003). Over 90% of these fish spawn in main-stem sections of the river (Stober et al. 1982). Pink salmon life history characteristics in the study area are typical of most populations found in Washington (Table 2). The heaviest spawning occurs in the 16 mi of river directly below Gorge Powerhouse.

In the Skagit River, there are three stocks of naturally reproducing chum salmon, all of which are fall-run fish (WDFW et al. 1994). The spawn timing and other early life history attributes are similar to those of most other fall chum salmon populations in western Washington (Table 2). Preferred spawning habitats of chum salmon include side channels, sloughs, and shallow, lower-velocity, protected areas along the margins of the main channel (Stober et al. 1982). The abundance of chum salmon in the Skagit River is cyclical, with higher escapement observed during even-numbered years, when pink salmon are absent (WDFW et al. 1994). Chum salmon escapement levels for the basin typically range from 15,000 to 150,000. The majority of chum salmon in the Skagit River spawn at age 4, although 3-year-old fish may represent up to 50% of escapement during odd years (Salo 1991).

Methods

Flow data.—We quantified changes in redd protection resulting from changes in flows below the Skagit Hydroelectric Project by analyzing hourly and daily flow data from the U.S. Geological Survey (USGS) gauging station for the Skagit River at Newhalem (number 12178000). This gauge, which is located immediately downstream of the Gorge Powerhouse, best describes flows released by Gorge Dam and Powerhouse. Three time periods were evaluated: (1) prior to implementation of the interim agreement (1950–1980), (2) after implementation of the interim agreement (1981–1990), and (3) after implementation of the final agreement (1991–2001).

We calculated a number of flow characteristics for each of the three periods, including (1) the average daily flow during the spawning period of each salmon species, (2) the lowest flow during the incubation period of each species (Stober et al. 1982), and (3) the difference between average daily flow during spawning and the lowest daily flow during incubation.

The potential for egg and alevin dewatering can be reduced (i.e., redd protection increased) by increasing minimum flows during incubation and by minimizing the difference between spawning flows and corresponding incubation flows. We quantified changes in fry stranding protection levels by comparing the following flow fluctuation characteristics for each of the three periods: (1) the frequency of flow fluctuation (ramping) events during each month from February through June, when salmon fry are most abundant in the study area, (2) the average rate of change in flow during downramping conditions (i.e., downramp rate), and (3) the percentages of daytime versus nighttime downramping events.

Greater protection of fry from stranding is achieved by reducing the frequency of flow fluctuations, the downramp rate, and the number of daytime downramping events.

Spawner data.—Spawner data were collected by WDFW fisheries biologists as part of annual salmon escapement surveys (WDFW 2003). Salmon escapement data are obtained on a reach-level basis in Puget Sound rivers (WDFW et al. 1994). These data are collected as a census, with field crews counting the total number of spawners within a reach during each year. Chinook salmon redds were counted from a helicopter, and census data were available from 1952 to 1998, with the exception of 1997. Census data for 1999–2002 were also not available. Pink salmon carcass counts originated from combined boat and foot surveys conducted from 1959 to 2001. Chum salmon spawner and carcass counts from combined boat and foot surveys were available for the years 1974–1996. The study area was segregated into three reaches for the spawner and redd surveys: (1) Newhalem to the confluence of the Cascade River (reach 1; length = 16 mi), (2) the Cascade River to the confluence of the Sauk River (reach 2; 11 mi), and (3) the Sauk River to the confluence of the Baker River (reach 3; 10 mi). Reach start and end points corresponded with those historically used by the WDFW to construct the spawner database. Spawner surveys were based on the same methodology each year, and were completed by the same WDFW biologist after 1974.

For censuses of spawning chum salmon, the WDFW further divided reach 1 into two discrete subreaches that represented a 9-mi-long upper subreach and a 7-mi-long lower subreach. Spawner abundance values were calculated as densities (fish/mi, carcasses/mi, or redds/mi) for the purposes of this study.

Multiple spawner surveys were usually completed by WDFW each year to better determine the peak numbers of Chinook, pink, and chum salmon spawners within each reach (Olson and Knutzen 1997). The number of spawner surveys conducted during a given year varied from 1 to 9 per reach for Chinook salmon, from 1 to 13 per reach for pink salmon, and from 1 to 8 per reach for chum salmon. For each year in which multiple spawner surveys were completed, we selected the highest spawner count for each species for inclusion in our analyses. The spawner data should therefore be considered peak counts for the spawning period rather than the absolute number of spawners present in a given reach. For each year in which only one spawning survey was conducted, we confirmed that the survey occurred near the known peak of spawning activity in the Skagit River. However, counts derived from single-survey years are probably less accurate than those obtained from multiple-survey years. Nevertheless, the high spawner counts we used were drawn from the same data set used to derive escapement estimates and trends for the study area and were therefore the best measure of spawner abundance (WDFW et al. 1994). We used spawner count data to examine possible changes in the distribution and density of salmon within the study area for two time periods: before flow conditions were modified (pre-agreement) and afterward (postagreement, which included interim and final agreement periods). We combined the interim and final agreement periods to represent a single period of modified flow instead of two shorter periods.

Escapement trend data.—We obtained yearly escapement data for salmon spawning within major Skagit River subbasins, including the study area, the lower Skagit River, and the Sauk River, and within unregulated subbasins of neighboring Puget Sound rivers, including the Stillaguamish, Skykomish, and Snohomish rivers. Escapement data for pink, chum, and Chinook salmon were obtained from the salmon and steelhead stock inventory database (WDFW 2003). Basin escapement values for the Puget Sound rivers were calculated from census data obtained from spawner surveys conducted on a reach-level basis (WDFW et al. 1994). Reaches typically ranged from 10 to 30 mi in length. Total escapement was calculated for each subbasin by multiplying reach-level counts by an expansion factor that represented the ratio between the total spawning area in a basin and the area of the spawning census reach. These subbasin and basin escapement data are used by state, federal, and tribal biologists to evaluate spawner population trends for each river. All of the subbasins we selected for comparison with the study area had native, naturally reproducing salmon runs with minimal influence from hatchery stocks (WDFW et al. 1994). Neighboring rivers that were heavily impacted by urban development (e.g., the Nooksack, Cedar, Duwamish, and Green rivers) were excluded from trend analysis.

Statistical analysis.—We employed a before-and-after impact comparison (Green 1979) to analyze the effects of the implemented flow measures on the abundance of spawning salmon within the study area. Changes in spawner abundance before and after implementation of interim and final flow agreements and differences among the study reaches were evaluated by use of a factorial analysis of variance (ANOVA). We used a general linear modeling statistical procedure because the spawner density data were unbalanced (i.e., different numbers of observations for each ANOVA factor). The number of years of available spawning survey data before and after implementation of the interim agreement were not the same for the three salmon species. Also, during some years, the three study reaches were not all surveyed. The spawner density data were log-transformed prior to analysis to normalize and homogenize the variances. For chum and Chinook salmon, we completed a three-way ANOVA on spawner density based on reach, time period, and year type (odd or even years). For pink salmon, a two-way ANOVA of spawner density was completed based on reach and time period; all data were from odd years. Longitudinal differences in salmon spawner density were evaluated by comparing mean spawner or redd densities among the three reaches. Only a few chum salmon spawner surveys were conducted by WDFW in reach 3 because relatively few chum salmon spawn there. Chum salmon spawning data for reach 3 were insufficient (three observations within the period of record) for inclusion in the statistical analysis. However, chum salmon spawner data were collected in two subreaches of reach 1 (1A and 1B), and these data were included in the analysis. Changes in salmon spawner density in the study area were evaluated according to two time periods: before implementation of the interim flow agreement (pre-1981) and after implementation (post-1981). The flow changes that began in 1981 did not affect returns of Chinook salmon and chum salmon until 1985 due to their 4-year life cycles. The effect on pink salmon, which have a 2-year life cycle, began in 1983. We defined a significance level α of 0.10 for all statistical analyses. Statistical differences within ANOVA factors were evaluated by use of Fisher's least-significant-difference test (Steel and Torrie 1980).

The number of spawner surveys conducted within a given reach varied from year to year. The number of spawner surveys conducted within a given year was determined by WDFW fish biologists and was influenced by flow conditions, water visibility, and other factors. The variability in the annual number of spawning surveys was a potential source of bias in our statistical analysis if total survey numbers and spawner counts were related. To address this potential problem, we completed a three-way ANOVA on spawner density, with reach, time period, and total survey number as factors. We used this analysis to determine whether the number of surveys significantly affected spawner density and whether a significant interaction existed between total survey number and time period.

We calculated spawner escapement trends for the study area to determine whether reach-level changes in spawner abundance could be detected between pre- and postagreement periods. We also compared spawner escapement trends in the study area with those in other Skagit River subbasins and in unregulated subbasins in neighboring rivers. Escapement trends were calculated with exponential linear regression based on the same statistical procedure employed by the National Marine Fisheries Service to evaluate salmon population trends (Meyers et al. 1998; NMFS 1999). The comparison of subbasins allowed us to better determine whether trends observed in the study area were caused by within-basin factors such as changes in flow management, or by large-scale factors like climate and ocean productivity changes, which would produce similar trends in neighboring rivers.

We used linear regression to examine potential relationships between flow and spawner abundance in the study area. We tested for correlations between flow characteristics of the spawning and incubation periods with spawner abundance observed 2 years later (pink salmon) or 4 years later (Chinook and chum salmon). These lag times corresponded to the predominant life cycle (spawning to adult return) of each species in the Skagit River. Linear regression analysis was used to examine

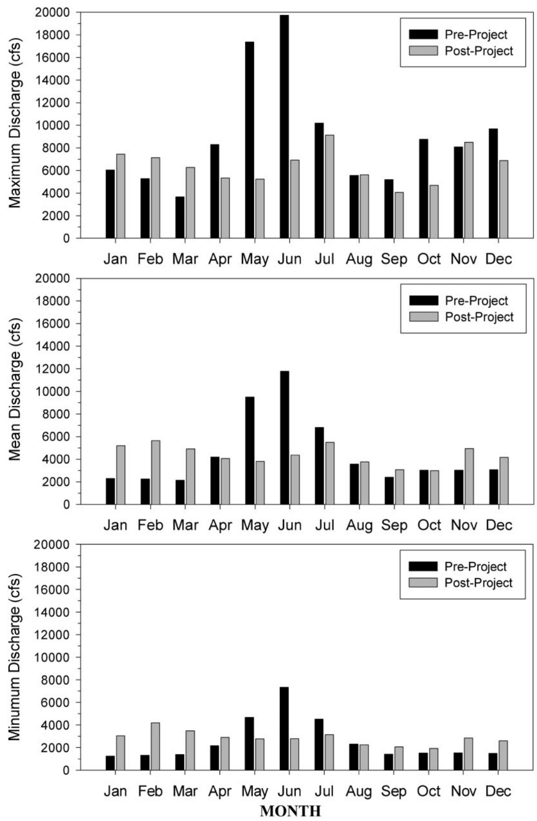

FIGURE 2.—Average values of monthly maximum, mean, and minimum discharge (cubic feet per second [cfs]) in the Skagit River at Newhalem, Washington, downstream of the Skagit Hydroelectric Project. Flows under preproject (1909–1930) and postproject (1981–2001) conditions.

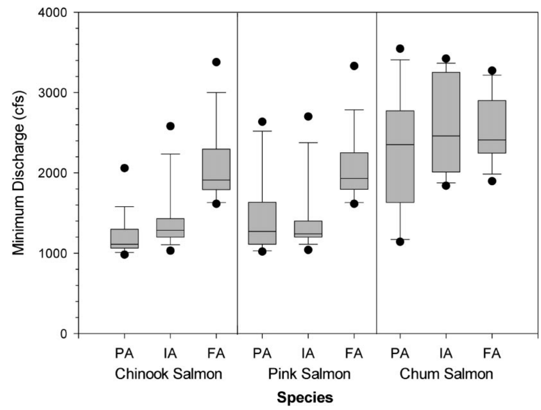

FIGURE 3.—Frequency plots of annual minimum flows (cubic feet per second [cfs]) within the upper Skagit River, Washington, downstream of the Skagit Hydroelectric Project during the incubation of Chinook, pink, and chum salmon. Minimum flows were changed as part of Federal Energy Regulatory Commission relicensing agreements, and are plotted under pre-agreement (PA), interim agreement (IA), and final agreement (FA) conditions. The top and bottom of each box represent the 75th and 25th percentiles, the line within the box represents the median, the bars indicate the 90th and 10th percentiles, and the points denote the 95th and 5th percentiles.

possible relationships between incubation flows and spawner abundances for pink and Chinook salmon. Chum salmon spawners in the Skagit River are substantially more abundant in even years than in odd years. For this reason, an analysis of covariance (ANCOVA) was completed to evaluate the relationship between incubation flow and chum salmon spawner abundance while controlling for variation between year types.

Results

Changes in Flows

The Skagit Hydroelectric Project resulted in many changes to the natural flow regime of the upper Skagit River. The seasonal storage and release of water by Ross Reservoir for power generation were mainly responsible for these changes. Major flow changes from pre-project conditions included reductions in mean and maximum flows during the snowmelt runoff period (April–July) and increases in minimum and mean flows during the fall and winter (Figure 2).

Under the interim agreement (1981–1990), minimum flows during the incubation periods of Chinook and pink salmon increased slightly compared with pre-agreement conditions (Figure 3). Minimum incubation flows during dry years (as measured by 10th percentile annual flow) increased by 155 cfs for Chinook salmon and by 135 cfs for pink salmon under the interim agreement compared to pre-agreement conditions. Flow increases under the interim agreement were greatest for the incubation period of chum salmon, with minimum flows increasing by 720 cfs during dry years. Minimum flows increased substantially during the incubation periods of all three salmon species under the final agreement (1991–2001) from pre-agreement conditions (Figure 3). Minimum flows during dry years increased by 664 cfs for Chinook salmon, 624 cfs for pink salmon and 864 cfs for chum salmon under final agreement conditions, compared with pre-agreement conditions. Under normal (i.e., median) flow conditions, minimum incubation flows increased by 800 cfs for Chinook salmon, 660 cfs for pink salmon, and 60 cfs for

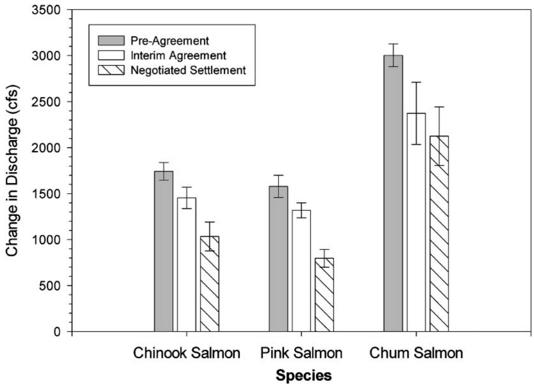

FIGURE 4.—Average difference between daily spawning flow (cubic feet per second [cfs]) and minimum incubation flow (±SE) for Chinook, pink, and chum salmon in the upper Skagit River, Washington, downstream of the Skagit Hydroelectric Project. Flows were changed as part of Federal Energy Regulatory Commission relicensing agreements; data are presented for pre-agreement, interim agreement, and final agreement conditions. Data are from the U.S. Geological Survey gauging station on the Skagit River at Newhalem.

chum salmon compared to pre-agreement conditions.

Differences between spawning flows and minimum incubation flows progressively declined during the interim and final agreement periods (Figure 4). Pink salmon experienced the largest reduction (50%) in the mean difference between daily spawning flows and minimum incubation flows. Chinook and chum salmon experienced reductions of 41% and 29%, respectively, in the difference between spawning and minimum incubation flows.

The number of downramping events during fry emergence and outmigration periods substantially declined and the percentage of daytime downramping was greatly reduced after interim and final agreements were implemented (Table 3). The average number of downramping events during the period of peak fry stranding (February 1–May 31) declined by 48% from the pre-agreement period. Prior to the interim agreement, daytime downramping represented 89% of all events occurring during the period of peak stranding. Daytime downramping fell to 40% under the interim agreement and to 3% under the final agreement. The average downramp rate increased by 63% between pre-agreement and final agreement periods (Table 3). The average downramp rate increased to 950 cfs/h during the final agreement period, but was still well below the allowable maximum of 3,000 cfs/h. A close examination of downramp rates from the interim and final agreement periods revealed that more than 99% of the values were below 3,000 cfs/h.

The Skagit Hydroelectric Project achieved a high level of operational compliance with the flow conditions set forth under the final agreement. Compliance with minimum flow, downramping, and amplitude conditions (Table 1) exceeded 99%; violations were limited to rare equipment failures or to threshold hydrological events (e.g., rapidly changing natural inflows), which are allowed for under the agreement.

Spawner Distribution and Abundance

Pink salmon.—Carcass densities of pink salmon differed significantly among the three study reaches ($P < 0.05$), and significantly increased between the pre- and postagreement periods ($P < 0.05$) (Figure 5). Carcass density increases were greatest in the reach closest to the source of flow management (reach 1) and declined with distance downstream. This spatial shift in spawner density was statistically significant ($P < 0.10$) as measured by the reach × time interaction. Average carcass density in reach 1 increased by 276%, from 311 carcasses/mi before 1983 to 1,169 carcasses/mi after 1983. In reach 2, average density increased by 231%, from 171 carcasses/mi before 1983 to 566 carcasses/mi after 1983. In contrast to reaches 1

TABLE 3.—Average annual downramping (flow reduction) parameters in the Skagit River, Washington, downstream of the Skagit Hydroelectric Project. Parameters for the interim flow agreement (1981–1990) and final flow agreement (1991–2001) periods are compared with pre-agreement conditions (1976–1980). The downramp amplitude is the difference between the highest and lowest flow releases during a given 24-h period. Flows are expressed in cubic feet per second (cfs). Data are from the U.S. Geological Survey gauging station for the Skagit River at Newhalem.

Conditions	Number of downramping events	Daytime downramping events (%)	Average downramp amplitude (cfs)	Average downramp rate (cfs/h)
Pre-agreement	186	89	1,762	583
Interim agreement	151	40	1,760	718
Final agreement	90	3	1,760	950

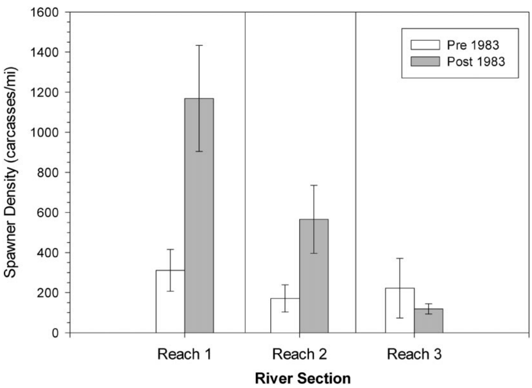

FIGURE 5.—Mean density of pink salmon spawner carcasses (±SE) in odd-numbered years during 1959–1981 (pre-1983) and 1983–2001 (post-1983) within three reaches of the upper Skagit River, Washington, downstream of the Skagit Hydroelectric Project.

and 2, average density in reach 3 decreased by 46% from the pre-1983 period (222 carcasses/mi) to the post-1983 period (119 carcasses/mi). The differences in average carcass density before and after 1983 were significant for reaches 1 and 2 (least significant difference; $P < 0.05$) but not for reach 3.

Chum salmon.—Average counts of chum salmon spawners were significantly different ($P < 0.05$) among the three study reaches, increased significantly between the two time periods ($P < 0.001$), and differed significantly between year types ($P < 0.001$) (Figure 6). Like pink salmon, chum salmon spawners increased substantially in density after implementation of the flow agreements. Increases in chum salmon spawner densities were proportionately greatest in reach 1B, and the reach × time period interaction was significant ($P < 0.05$). Increases in the absolute number of chum salmon spawners were greatest during even years. Average spawner density in reach 1A during odd years increased by 1,817%, from 6 fish/mi before 1985 to 115 fish/mi after 1985. Average spawner density in reach 1B during odd years increased by 239%, from 38 fish/mi before 1985 to 129 fish/mi after 1985. Average spawner density in reach 1A during even years increased by 697%, from 58 fish/mi before 1985 to 462 fish/mi after 1985. In reach 1B, spawner density during even years increased by 242%, from 326 fish/mi before 1985 to 1,116 fish/mi after 1985. The difference in spawner density between time periods was statistically significant within reaches 1A and 1B (least significant difference; $P < 0.05$) but not within reach 2. In reach 2, chum salmon spawner

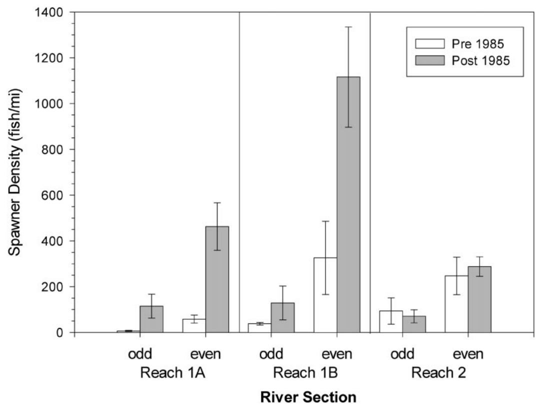

FIGURE 6.—Mean density of chum salmon spawners (±SE) in odd- versus even-numbered years during 1968–1984 (pre-1985) and 1985–1996 (post-1985) within three reaches of the upper Skagit River, Washington, downstream of the Skagit Hydroelectric Project.

density during even years slightly increased between the pre- and post-1985 periods, from 247 to 288 fish/mi (17% increase). Spawner density in reach 2 during odd years decreased from 93 to 70 fish/mi (25% decline) between the two periods.

Chinook salmon.—Redd densities of Chinook salmon were significantly different among the three study reaches ($P < 0.01$) and between year types ($P < 0.05$) but not between time periods ($P = 0.35$) (Figure 7). Chinook salmon redd density increased progressively upstream, the highest densities being observed in reach 1. Redd densities in reaches 1 and 2 were significantly greater in even years than in odd years (least significant differ-

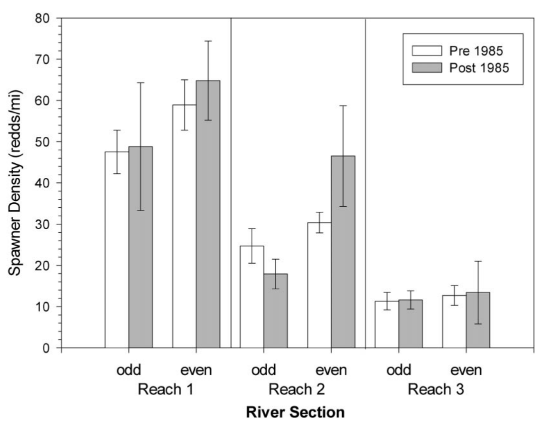

FIGURE 7.—Mean density of Chinook salmon redds (±SE) in odd- versus even-numbered years during 1952–1984 (pre-1985) and 1985–1998 (post-1985) within three reaches of the upper Skagit River, Washington, downstream of the Skagit Hydroelectric Project.

TABLE 4.—Summary of escapement trends for native, odd-year-spawning pink salmon in the northern Puget Sound region, Washington. Escapement for the upper Skagit River was calculated based on carcass counts in reaches 1 and 2 downstream of the Skagit Hydroelectric Project. All other data are from WDFW (2003).

	1959–1981 escapement			1983–2001 escapement			
Location	Trend (% per year)	Mean	SE	Trend (% per year)	Mean	SE	Change in escapement between time periods (%)
Upper Skagit River	5.6	6,401	2,024	6.0	23,469	5,337	267
Lower Skagit River	−2.5	297,667	74,578	1.1	482,106	93,905	62
Stillaguamish River	−8.5	140,750	48,513	1.0	205,250	65,275	46
Snohomish River	0.4	121,300	18,482	2.2	252,250	93,892	108

ence; $P < 0.05$). The greatest difference in redd density between the pre- and postagreement periods was observed in reach 2 during even years: densities were 30 redds/mi before 1985 and 47 redds/mi after 1985 (57% increase). In reach 2 during odd years, redd density declined from 25 redds/mi before 1985 to 18 redds/mi after 1985 (28% decrease).

Effect of Number of Surveys per Year

The annual number of surveys did not significantly influence the comparisons of mean spawner density among study reaches and between time periods. Survey number did not explain a significant amount of variation in the spawning densities of pink salmon ($P = 0.77$), chum salmon ($P = 0.14$), or Chinook salmon ($P = 0.32$). The survey number × time period interaction was not significant for pink salmon ($P = 0.68$), chum salmon ($P = 0.84$), or Chinook salmon ($P = 0.69$).

Escapement Trend Comparisons among Subbasins

Pink salmon.—Mean pink salmon escapement in the upper Skagit River increased by 267% from the pre-agreement period to the postagreement period (Table 4). Mean escapement increased from 6,401 fish (1959–1981) to 23,469 fish (1983–2001). The increase in escapement between the two periods was substantially greater in the study area than in the Skagit River basin (62%; total basin escapement) or the neighboring Stillaguamish (46%) and Snohomish (108%) river basins. Pink salmon escapement trends from 1983 to 2001 were positive in all the north Puget Sound basins evaluated; the greatest increase was observed in the study area at 6.0% per year (Table 4). Escapement trends from 1959 to 1981 were negative in the Skagit and Stillaguamish river basins, with annual decreases of 2.5% in the Skagit River basin and 8.5% in the Stillaguamish River basin. Due to the spatial shift in pink salmon spawner abundance towards the upper reaches of the Skagit River, total escapement numbers for the Skagit River basin might be underestimated for recent years (Hard et al. 1996).

Chum salmon.—Chum salmon escapement levels increased overall in the Puget Sound region during 1985–2001. The increase in chum salmon escapement was higher in the study area than in other Puget Sound rivers (Table 5). Mean escapement in the study area increased from 3,028 fish (1974–1984) to 7,411 fish (1985–2001), an increase of 145%. In comparison, the number of spawners declined in the Skagit River basin (−3%; total escapement) and the Sauk River (−9%). Chum salmon escapement increased between the

TABLE 5.—Summary of escapement trends for native fall-run chum salmon in the northern Puget Sound region, Washington. Escapement for the upper Skagit River was calculated based on live and dead spawner counts for reaches 1 and 2 downstream of the Skagit Hydroelectric Project. All other data are from WDFW (2003).

	1974–1984 escapement			1985–2001 escapement			
Location	Trend (% per year)	Mean	SE	Trend (% per year)	Mean	SE	Change in escapement between time periods (%)
Upper Skagit River	−29.8	3,028	1,123	5.2	7,411	1,886	145
Lower Skagit River	−12.5	62,758	17,567	0.0	61,072	9,808	−3
Sauk River	−8.8	8,320	2,127	−1.8	7,607	1,808	−9
Stillaguamish River	−0.6	23,973	6,728	3.6	49,443	10,398	106
Skykomish River	6.1	20,397	5,300	3.2	35,386	6,474	73

TABLE 6.—Summary of escapement trends for native summer–fall Chinook salmon in the northern Puget Sound region, Washington. Data are from WDFW (2003).

Location	1974–1984 escapement			1985–2001 escapement			Change in mean escapement between time periods (%)
	Trend (% per year)	Mean	SE	Trend (% per year)	Mean	SE	
Upper Skagit River	−0.7	7,521	676	−0.5	7,745	878	3
Lower Skagit River	−3.3	3,286	334	−4.3	1,939	278	−41
Sauk River	−5.1	1,331	196	−5.2	634	92	−52
Stillaguamish River	−12.5	832	127	0.3	856	76	3
Skykomish River	−9.9	1,396	206	−4.5	822	106	−41

two time periods in the Stillaguamish River (106%) and the Skykomish River (73%). The escapement trend for 1985–2001 was highest in the study area; spawner numbers increased at 5.2% per year. In comparison, zero growth in escapement was observed for the entire Skagit River basin and negative growth (−1.8% per year) was observed for the Sauk River during this same period. Escapement increases of 3.6% and 3.2% per year were observed in the Stillaguamish and Skykomish rivers, respectively. Escapement trends in the study area during 1974–1984 were highly negative (−29.8% per year), and therefore this subbasin showed the greatest improvement between the two time periods (Table 5).

Chinook salmon.—Chinook salmon spawner escapement in the upper Skagit River exhibited short- and long-term stability compared with other Skagit River subbasins(Table 6). Mean escapement values for upper Skagit River summer–fall Chinook salmon were 7,521 fish during 1974–1984 and 7,745 fish during 1985–2001 (3% increase). In comparison, summer–fall Chinook salmon escapement substantially decreased in the lower Skagit (−41%) and Sauk rivers (−52%) between the two periods. Spawner escapement also substantially declined in the Skykomish River (−41%). In addition to the study area, only the Stillaguamish River maintained relatively stable mean escapement values for summer–fall Chinook salmon between 1974–1984 and 1985–2001. The escapement trend for the study area from 1985 to 2001 was negative (–0.5% per year). The decline was small compared with those observed in the lower Skagit River (−4.3% per year) and the Sauk River (−5.2% per year). Summer–fall Chinook salmon escapement trends in the study area were correlated to those observed in the lower Sauk River ($r = 0.44$; $P < 0.05$), a major tributary of the Skagit River, as well as to summer–fall Chinook salmon escapement in the lower Skagit River ($r = 0.52$; $P < 0.05$). However, summer–fall Chinook salmon escapement trends in the Sauk and lower Skagit rivers were substantially lower than trends observed in study area. Because the number of spawners in the study area did not significantly change between pre- and postagreement periods, in contrast with other areas of the watershed, this reach provided a larger and increasing proportion of the total summer–fall Chinook salmon escapement in the Skagit River basin (Table 7). The proportion of Skagit River basin summer–fall Chinook salmon supported in the study area was 62% during 1974–1984, 73% during 1985–1994, and 78% during 1995–2001. The increases in spawner proportion among these three time periods were statistically significant (one-way ANOVA; $P < 0.01$). For the entire Skagit River basin, average escapement fell 17.8% between the pre-agreement and interim agreement periods and was 5.1% below the pre-agreement level during the final agreement period (Table 7). For the study area, escape-

TABLE 7.—Average escapement of summer–fall Chinook salmon in the upper Skagit River, Washington (reaches 1 and 2), compared with total escapement in the Skagit River basin. Escapement values for the interim flow agreement (1985–1994) and final flow agreement (1995–2001) periods during Skagit Hydroelectric Project relicensing are compared with escapement during the pre-agreement period (1974–1984). Data are from WDFW (2003).

Study period	Skagit River basin		Study area		Study area proportion of total basin escapement (%)
	Escapement	SE	Escapement	SE	
Pre-agreement	12,139	1,002	7,521	676	62
Interim agreement	10,279	1,561	7,504	1,180	73
Final agreement	11,527	1,978	8,805	1,411	78

ment levels fell only by 0.2% during the interim agreement period and increased by 17.1% during the final agreement period.

Relationships between Flows and Spawner Abundance

Pink salmon spawner densities were negatively correlated with the difference between average daily spawning flow and the corresponding minimum incubation flow recorded 2 years earlier. The relationship was curvilinear and was best fit by a log–log regression ($R^2 = 0.46$, $P < 0.01$). Spawner abundance was predicted to increase as differences between spawning and incubation flows are reduced.

Chum salmon spawner densities in the study area were positively and significantly correlated with increases in the minimum incubation flow recorded 4 years earlier. The relationship was determined by ANCOVA of two factors (total $R^2 = 0.55$): the minimum incubation flow 4 years earlier ($P < 0.01$) and year type ($P < 0.001$). This relationship predicts that spawner abundance increases with increasing minimum incubation flow but varies significantly between odd and even years.

Discussion

The negative effects of flow fluctuations on fish populations below hydroelectric facilities have been well documented (Graybill et al. 1979; Ward and Stanford 1979; Stober et al. 1982; Petts 1984; Cushman 1985; Bain et al. 1988). The irregular daily flow patterns and unnatural seasonal flow patterns that often occur below hydroelectric dams can create numerous adverse impacts on the abundance and diversity of fish, including reduced availability of the shallow margin habitat required by many riverine species (Kingsolving and Bain 1993), dewatering of spawning areas during the incubation period, and stranding of juveniles along channel margins (Hunter 1992; Freeman et al. 2001). The impacts caused by flow fluctuations are typically greatest in the reach immediately below a project and decline with distance downstream (Pflug and Mobrand 1989; Kingsolving and Bain 1993).

Few studies have examined the long-term responses of fish populations to modified flow regimes below hydroelectric dams (Freeman et al. 2001). Modified flows were thought to contribute to record-high escapement levels for adult Chinook salmon in the Vernita Bar section of the Columbia River (Chapman et al. 1986), although postimplementation observations were limited to just 1 year. Increases in the size and abundance of spawning lake sturgeon *Acipenser fulvescens* were documented during a 2-year monitoring period in the Sturgeon River, Michigan, following operational changes at a hydroelectric facility to minimize flow fluctuation impacts (Auer 1996). Increases in the abundance and diversity of warmwater fishes were observed below a major dam on the Tallopoosa River, Alabama, for a 2-year period after implementation of an improved flow regime (Travenichek et al. 1995; Bain and Travnichek 1996). These latter studies identified effects of the flow management measures by comparing fish abundance in the regulated reach immediately below the project with a less-regulated reach downstream.

As was done in similar, previous studies, we compared the abundance of fish in the most-regulated reach immediately below the hydroelectric project with those in less-regulated reaches downstream. In addition, we compared spawner abundance in the study area before and after implementation of flow measures. The total period of evaluation for our study was 22 years for pink salmon (odd years only), 29 years for chum salmon, and 45 years for Chinook salmon. Finally, we compared trends in spawner abundance before and after implementation between our study area and other Skagit River subbasins or nearby unregulated Puget Sound rivers. This allowed us to better differentiate the effects of our flow management measures from those associated with long-term changes in ocean productivity, salmon harvest levels, rainfall patterns, and other large-scale factors.

Spawner Abundance Responses to Flow Measures

Pink salmon and chum salmon.—Our results indicate that the flow management actions implemented in 1981 and further improved in 1991 resulted in substantial increases in the number of adult pink and chum salmon spawning downstream of the Skagit Hydroelectric Project. The increases in spawner abundance were greatest within the 16-mi reach located immediately downstream of the project (reach 1). This reach was the most impacted by the low minimum flow releases, high-amplitude flow fluctuations, and daytime downramping events that occurred prior to 1981. Shifts in the abundance of pink and chum salmon spawners over time exhibited a longitudinal gradient effect; the greatest increase occurred in the upstream-most reach, and progressively lower increases were observed downstream. We did not observe postagreement increases in pink salmon spawner density in reach 3, which was located 27 mi downstream from the project and was therefore least impacted by project operations. Because pink and chum salmon spawner abundance in the lowermost reach did not increase over time, we can assume that the increases observed in the uppermost reach probably resulted from the implemented flow improvements. A similar longitudinal response was observed in the abundance of warmwater fish below a major hydroelectric project on the Tallopoosa River after flow improvements were implemented (Freeman et al. 2001).

The increases in pink and chum salmon spawner abundance we observed downstream of the project imply that the egg-to-fry life history stages benefited from the flow management actions undertaken since 1981. The redds of pink salmon and chum salmon are highly vulnerable to dewatering because they are located along the shallow channel margins of the Skagit River (Stober et al. 1982). Increases in egg-to-fry survival rates of these two species within the study area can partly explain the postagreement increases in adult abundance. Our flow data demonstrate a significant improvement in the amount of dewatering protection provided to pink and chum salmon redds (Figure 4), which would in turn result in higher egg-to-fry survival. The risk of redd dewatering decreases as the difference between spawning and minimum incubation flows becomes smaller. High levels of protection for pink and chum salmon redds were achieved by substantially reducing the difference in spawning and incubation flows, allowing a high percentage of redds to remain wetted through fry emergence. Both pink and chum salmon utilize much shallower spawning habitat than Chinook salmon (Stober et al. 1982), and consequently received the greatest benefits from increases in minimum incubation flows.

Our results suggest that egg-to-fry survival rates declined with increasing distance downstream from the project. This might be explained by the reduction in the frequency and magnitude of flood flows in those reaches closest to the hydroelectric project, which includes a large storage reservoir (Ross Lake). The influence of peak flow events during incubation on the egg-to-migrant survival of Skagit River salmon was well documented by Seiler et al. (2001). That study demonstrated a strong negative relationship between peak flow and egg-to-migrant survival and suggested that peak flows cause widespread gravel scour to salmon redds, resulting in high levels of egg and fry mortality. Chinook salmon egg-to-migrant survival rates in the Skagit River ranged from 3% to 18%; survival rates decreased exponentially with increasing peak flow levels (Seiler et al. 2001). Within our study area, the greatest protection of salmon eggs and fry from peak flows occurs immediately below the project and then decreases downstream due to inflows from tributaries with natural peak runoff patterns. This relationship provides a plausible explanation why the highest densities of spawning pink and chum salmon were observed in the upstream-most reach, and why substantially lower spawner densities were observed in the downstream reaches. Because adult salmon typically return to their natal spawning grounds, we would expect reaches with the highest egg-to-fry survival rates to attain the highest spawner densities over time, provided that habitat conditions remain constant.

Reductions in salmon fry stranding and resulting improvements in fry survival rates may have also contributed to the increased abundance of spawning pink and chum salmon in the study area. The reductions in fry stranding rates were achieved by reducing the frequency of flow fluctuations, slowing the rates of change during downramping and reducing the proportion of daytime downramping events. These flow improvements effectively reduced the number of newly emerged pink and chum salmon fry stranded on gravel bars in the Skagit River study area (Pflug and Mobrand 1989). Increased fry survival rates occurred in two distinct stages: the first during the interim period when flows where initially modified and the second during the final agreement period when flows were modified again to further reduce fry stranding. The greatest improvements in fry survival rates likely occurred in reach 1. The reach's proximity to the hydroelectric project meant that it received the greatest impact of the adverse flow fluctuations that were present during the preagreement period. Reach 1 also possesses the wide, shallow gravel bars where fry are most susceptible to stranding. Stranding rates decline downstream due to flow attenuation and the increasing influence of tributary inflows with natural flow characteristics.

The greatest increases in chum salmon spawner abundance in reaches 1A and 1B occurred during even years. In contrast, chum salmon spawner abundance in reach 2 was not significantly different between even and odd years. Because pink salmon only spawn in the Skagit River during odd years, these results imply a negative effect of pink salmon on the abundance of spawning chum salmon. This effect is not attributable to competition for spawning space or to destruction of chum salmon redds by pink salmon, because chum salmon spawn considerably later in the year than pink salmon. Consequently, this negative relationship likely involves competition between pink and chum salmon juveniles or compensatory mortality of chum salmon in favor of pink salmon within the lower river, estuary, nearshore marine environment, or ocean.

Salmon redds within the study area are monitored every 7–10 d during the spawning period to verify that the minimum flow regimes provided for under the final flow agreement achieve the desired high levels of protection from redd dewatering. Incubation flows are commonly adjusted in response to seasonal variations in tributary inflows to achieve full redd protection. Adjustments in minimum flows are possible because of the availability of water from Ross Lake. Without these voluntary adjustments, especially during drought periods, reductions in pink and chum salmon egg survival would likely occur. The adjustments are unique to the study area and are not possible elsewhere in unregulated portions of the watershed.

The postagreement increases in egg-to-fry survival rates are probably highest in the upstreammost sections of the study area, where flow fluctuations were the most severe during the preagreement period. The longitudinal gradient in flow fluctuation impacts that existed before the agreements may be partially responsible for the postagreement shift in spawning distribution. If egg-to-fry survival within the study area increases relative to unregulated portions of the watershed, a redistribution of spawners could conceivably occur over time, especially if harvest rates are not adjusted to account for differential survival rates. If the observed shift in spawning distribution continues, we speculate that currently viable pink and chum salmon spawning and rearing habitat located in unregulated parts of the watershed could become underutilized if harvest rates are not adjusted. The genetic diversity of pink salmon and chum salmon stocks within the Skagit River watershed could be reduced over time if the spawning distribution shift continues.

Pink salmon spawner density was negatively correlated ($r = -0.68$; $P < 0.01$) with the difference between spawning and incubation flows 2 years earlier. This finding suggests a cause-and-effect relationship between downramping during the incubation period and the abundance of returning adults. The spawning behavior of pink salmon supports such a relationship, since this species spawns in shallower areas than other salmon species in the Skagit River. Consequently, pink salmon redds are the most vulnerable to dewatering caused by downramping during incubation. The abundance of spawning chum salmon was positively correlated ($r = 0.74$; $P < 0.01$) with the minimum incubation flows measured 4 years earlier. This relationship is consistent with the spawning requirements of chum salmon in the Skagit River. Side channels comprise a significant part of the chum salmon spawning areas in the Skagit River (Graybill et al. 1979). Egg and embryo survival in these side channels probably improves under higher sustained base flows, which maintain a greater level of hydraulic connectivity between the side channels and the main channel. The flow measures implemented in the study area have thus benefited chum salmon populations by improving channel connectivity.

Chinook salmon.—Chinook salmon spawner densities in reaches 1 and 2 were not significantly affected by flow management actions. As with pink and chum salmon, Chinook salmon spawner density progressively decreased from upstream to downstream, the highest number of spawners being observed in reach 1. However, the postagreement increases in Chinook salmon spawners within reaches 1 and 2 were small compared to those observed for pink and chum salmon and were not statistically significant. The longitudinal decline in Chinook salmon spawner density indicates either that spawning habitat was better in reach 1 than in reaches 2 and 3 or that egg and fry survival rates were highest in reach 1. The three reaches had similar habitat characteristics, and all contained an abundance of clean gravel and cobble suitable for Chinook salmon spawning. Declining Chinook salmon escapement trends in the other major Skagit River subbasins, the Sauk and lower Skagit rivers (Table 6), suggest that egg-to-fry survival rates were highest in the study area just below the hydroelectric project.

Chinook salmon within the study area typically spawn in relatively fast and deep water towards the center of the channel (Stober et al. 1982). This preference explains why the number of Chinook salmon spawners did not increase to the same extent observed in pink and chum salmon. Deeper spawning habitats within the study area are much less likely to become dewatered by minimum flows resulting from project operation or by seasonal reductions in tributary inflows. This explanation is consistent with the findings of previous studies on the effects of flow improvement measures by hydroelectric projects on fish abundance. The greatest impacts of flow fluctuations below hydroelectric projects are on species that primarily spawn in shallow marginal areas of the river channel (Bain et al. 1988; Travnichek and Maceina 1994). Consequently, flow improvements induce the greatest abundance responses in warmwater fish species that require shallow habitat for spawning and early life stages (Travenichek et al. 1995; Bain and Travnichek 1996). Species typically found in deeper water did not show the same increases in abundance as shallow-habitat-dependent species after implementation of flow measures by hydroelectric facilities in the southern USA (Bain and Travnichek 1996). The changes in abundance we observed for fish species that spawn in shallow water (pink and chum salmon) versus deep water (Chinook salmon) were similar to the responses observed in the previous studies of warmwater fish communities.

The longitudinal trend in Chinook salmon spawner abundance within the study area may reflect higher egg and fry survival rates resulting from project-related flood protection. Flood protection benefits to Chinook salmon redds should be greatest immediately below the project, where flood peaks are most reduced and should decline progressively downstream in response to increasing flood peaks caused by tributary inflows. Ross Lake typically captures all but the largest flood flows that occur during the September–April egg incubation period. Flood-induced channel scour impacts on salmon redds increase in a downstream direction due to tributary inflows, including those of the Cascade and Sauk rivers. The flood control capability in the study area reduces the impact of channel scour on spawning habitat, providing an additional level of protection missing in unregulated parts of the watershed. Seiler et al. (2001) illustrated the importance of flood flows on the egg-to-migrant life stages of Skagit River Chinook salmon during the 1990s. Chinook salmon egg-to-migrant survival rates ranged from 1.2% to 3.8% in years with severe flood flows and from 10.2% to 16.7% in years of little or no flooding. The downstream decline in the number of Chinook salmon redds in our study area is consistent with declining egg-to-migrant survival rates resulting from the increasing peak flows of unregulated tributaries.

Stranding rates of Chinook salmon fry within the study area were substantially reduced after implementation of flow management actions at the Skagit Hydroelectric Project (Pflug and Mobrand 1989). Flow improvements, including reduced frequency of flow fluctuations and elimination of daytime downramping, contributed to increased survival of Chinook salmon fry prior to outmigration from the study area. These improvements reduced the number of Chinook salmon fry stranded on gravel bars during downramping (Pflug and Mobrand 1989).

Regional Escapement Trends

The increase in pink salmon spawner abundance within the study area during the 18-year postagreement period (1983–2001) was considerably greater (267%) than those observed for the entire Skagit River basin and for neighboring northern Puget Sound rivers (Table 4). The 27-mi study area supports the largest number of pink salmon spawners in the Skagit River basin (WDFW et al. 1994; Hard et al. 1996). Consequently, the increasing abundance of spawners within the study area is largely responsible for the increasing escapement trend calculated for the entire basin. The escapement trend in the Skagit River basin (1.1% per year) was substantially lower than that of the study area (6.0% per year), indicating that spawner abundance declined in other areas of the basin over this period. Escapement values increased in all of the northern Puget Sound rivers we evaluated, indicating that pink salmon populations increased regionally in response to favorable changes in ocean productivity, climate, or other large-scale factors. However, the increase in pink salmon spawner abundance within the study area was far greater than the increases within other areas, which suggests that local environmental factors, including the flow improvement measures, were largely responsible.

Chum salmon spawner abundance substantially increased (145%) in the study area during the 17-year postagreement period, whereas it declined in the Sauk River basin and the entire Skagit River basin (Table 5). Because the study area supports the largest number of chum salmon spawners in the Skagit River basin (WDFW et al. 1994), these results imply that the increases in spawner abundance in the study area have been important in sustaining basinwide escapement levels. These results also suggest that the proportion of Skagit River basin chum salmon that spawn in the study area increased over this period. Major increases in chum salmon escapement were observed in the neighboring Stillaguamish River (106%) and Skykomish River (73%), providing evidence for a regional increase during 1985–2001. However, the shift from a strongly negative escapement trend in the pre-agreement period to a positive escapement trend within the study area suggests that local factors, such as the flow improvement measures, were responsible for the observed increase in abundance. Prior to the implementation of the flow measures (1975–1984), chum salmon populations within the study area were severely declining (−29.8% per year) at a rate far greater than those concurrently observed in unregulated systems, including the Sauk and Stillaguamish rivers. After implementation of flow measures, chum salmon spawner escapement in the study area exhibited a positive trend (5.2% per year). This major reversal in chum salmon escapement trends indicates that the prior flow regime adversely affected chum salmon, and that the present flow regime is far more beneficial to this species.

Despite the long-term variability in Chinook salmon escapement in the study area, it is considered the healthiest native stock in the Puget Sound region (WDFW et al. 1994). Chinook salmon escapement in the study area remained relatively stable over time (3% increase per year), with only the Stillaguamish River showing similar trends between the pre- and postagreement periods (Table 6). In contrast, Chinook salmon escapement levels substantially declined in the lower Skagit River (−41%) and the Sauk River (−52%). The difference in population trends among the three major Skagit River subbasins resulted in an increasing proportion of summer–fall Chinook salmon spawning in the study area, culminating in 78% during the final agreement period (Table 7). Severe declines in Chinook salmon within other Puget Sound rivers resulted in the awarding of threatened status for the Puget Sound evolutionarily significant unit in 1999 (NMFS 1999).

Our results are encouraging and indicate that flow improvements have largely achieved the objectives established by the utility, state and federal agencies, and tribes. Flow management actions have contributed to improved rates of egg-to-fry survival and reduced rates of fry stranding, which in turn have resulted in improved spawner returns for pink and chum salmon and slowly increasing runs of summer–fall Chinook salmon.

Though our results are persuasive, they must be viewed with some caution, since the possibility exists that other environmental factors could have caused the spawner abundance changes observed in the study area. Abundance increases could have resulted from improved ocean conditions or declining harvest rates after 1981. However, the increases in pink and chum salmon spawner abundance were substantially higher in the study area than in other Puget Sound rivers, especially the lower Skagit River and the Sauk River. Moreover, the shifts in pink and chum spawner distribution within the study area could only have resulted from local environmental factors. The shifts were concurrent with increases in abundance; it is likely that both are attributable to the same factors. Therefore, local rather than regional factors are probably responsible for the abundance changes in the study area.

Local environmental factors that could affect spawner abundance include changes in gravel abundance and distribution, flooding, and increased releases of hatchery-reared fish. There is currently no evidence that gravel conditions changed in the upper river during the study period. Gravel inputs to the uppermost reach (reach 1) were reduced due to the trapping of gravel by the three upriver reservoirs. However, several tributaries located below the dams supply gravel to the study area channel. Gravel conditions probably did not substantially change in reach 1, yet this reach hosted the greatest increases in spawner abundance in the study area. Increases in hatchery-produced pink and chum salmon within the study area might explain the increase in spawner abundance. Because the spawners in the study area are derived from native and wild-spawning fish, hatchery releases have little influence on escapement (WDFW et al. 1994).

Conclusions

The flow measures implemented at the Skagit Hydroelectric Project in 1981 and improved in 1991 were developed to minimize the adverse impacts of project-related flow fluctuations on salmonid redds and fry. Our results indicate that flow measures targeted at improving salmon populations below hydroelectric projects can be highly successful. The implemented flow measures appear to have resulted in substantially increased pink and chum salmon abundances and in a sustained healthy population of Chinook salmon within the upper Skagit River. Documenting the success of flow improvement programs such as that implemented on the Skagit River is important for validating their effectiveness, substantiating their cost, and encouraging their use on other river systems. We believe that the success of flow measures can best be documented through long-term monitoring studies that include the collection of data before and after implementation. These studies should include comparisons with spatial controls (e.g., upstream versus downstream) and temporal controls (e.g., before and after implementation) to better differentiate the effects of the flow measures from those of external factors and regional trends. We hope that more information on the long-term benefits provided to salmon by flow management and other habitat restoration measures will be yielded by the widespread monitoring studies implemented in response to the listing of salmon and other fish species as threatened or endangered. The results of these studies will ultimately be needed to validate the success of the habitat protection and restoration measures used to improve salmonid populations throughout the Pacific Northwest.

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