

W. P. Connor and A. P. Garcia, United States Fish and Wildlife Service, P.O. Box 18, Ahsahka, Idaho 83520
email: william_connor@fws.gov

A. H. Connor, United States Forest Service, 12730 Highway 12, Orofino, Idaho 83544

E. O. Garton, Department of Fish and Wildlife, University of Idaho, Moscow, Idaho 83844-1136

and

P. A. Groves and J. A. Chandler, Idaho Power Company, 1221 Idaho Street, Boise, Idaho 83702

Estimating the Carrying Capacity of the Snake River for Fall Chinook Salmon Redds

Abstract

Recovery planning for imperiled populations of anadromous salmonids can require estimates of the carrying capacity of a river for redds (hereafter, redd capacity). We estimated redd capacity for the 106 known fall chinook salmon spawning sites in the upper and lower reaches of the Snake River. We used a modification of the Instream Flow Incremental Methodology to estimate spawning area (m^2) for 12 representative study sites. We estimated that one redd occupied $70 m^2$ of spawning area at the most heavily utilized site. Spawning area was estimated at the 12 study sites using a stable flow that was implemented to prevent redd de-watering, and two other flows that encompassed natural fluctuation. We estimated redd capacity for each study site by dividing the amount of spawning area modeled at each of the three flows by $70 m^2$. We input the redd capacity estimates for the study sites into the equation for a stratified random sample to make three estimates of redd capacity for all 106 known spawning sites. The estimates ranged between 2,446 and 2,570 redds. We conclude that the Snake River can support the 1,250 redds needed to satisfy Endangered Species Act de-listing criteria. However, annual surveys should be conducted to eventually determine if recruitment efficiency is affected by density dependent factors before the recovery goal is achieved.

Introduction

The construction of hydroelectric and diversion dams has eliminated or reduced spawning habitat used by anadromous salmonids in the Pacific Northwest (Wunderlich et al. 1994, Kondolf et al. 1996, Dauble and Geist 2000). Spawning habitat loss is one factor for the imperiled status of many anadromous salmonid stocks. The development of recovery plans for imperiled stocks sometimes requires estimating the number of redds that existing or lost habitat can carry (hereafter, redd capacity). This was the case with Snake River fall chinook salmon (*Oncorhynchus tshawytscha*), a stock that was listed as threatened under the Endangered Species Act (ESA) in 1992 (National Marine Fisheries Service 1992).

Snake River fall chinook salmon were displaced from the historic spawning area near Marsing, Idaho (Groves and Chandler 1999) by the construction of Brownlee, Oxbow, and Hells Canyon dams (Figure 1). By 1975, Lower Granite, Little Goose, Lower Monumental, and Ice Harbor dams impounded the lower 224 km of the Snake River leaving ~173 km of riverine spawn-

ing habitat between Hells Canyon Dam and the upper end of Lower Granite Reservoir (hereafter, the Snake River)(Figure 1). An estimate of redd capacity was needed to help define a recovery goal to match the remaining habitat. Few empirical data were available when the recovery plan was drafted, however, and biologists relied heavily on professional judgement to establish a proposed recovery goal of 2,500 adults (National Marine Fisheries Service 1995). The recovery goal equates to a redd capacity of 1,250 assuming an equal sex ratio for spawners.

While the Snake River fall chinook salmon recovery plan was being developed, we began to study spawners and their habitat. Water flow from Hells Canyon Dam was also stabilized at approximately $260 m^3/s$ during the spawning and incubation seasons to prevent redd de-watering (Groves and Chandler 1999). In this paper, we use data that were collected after the proposed recovery plan for Snake River fall chinook salmon was written to estimate fall chinook salmon redd capacity under a stable flow regime for two reaches of the Snake River. We also discuss the suitability

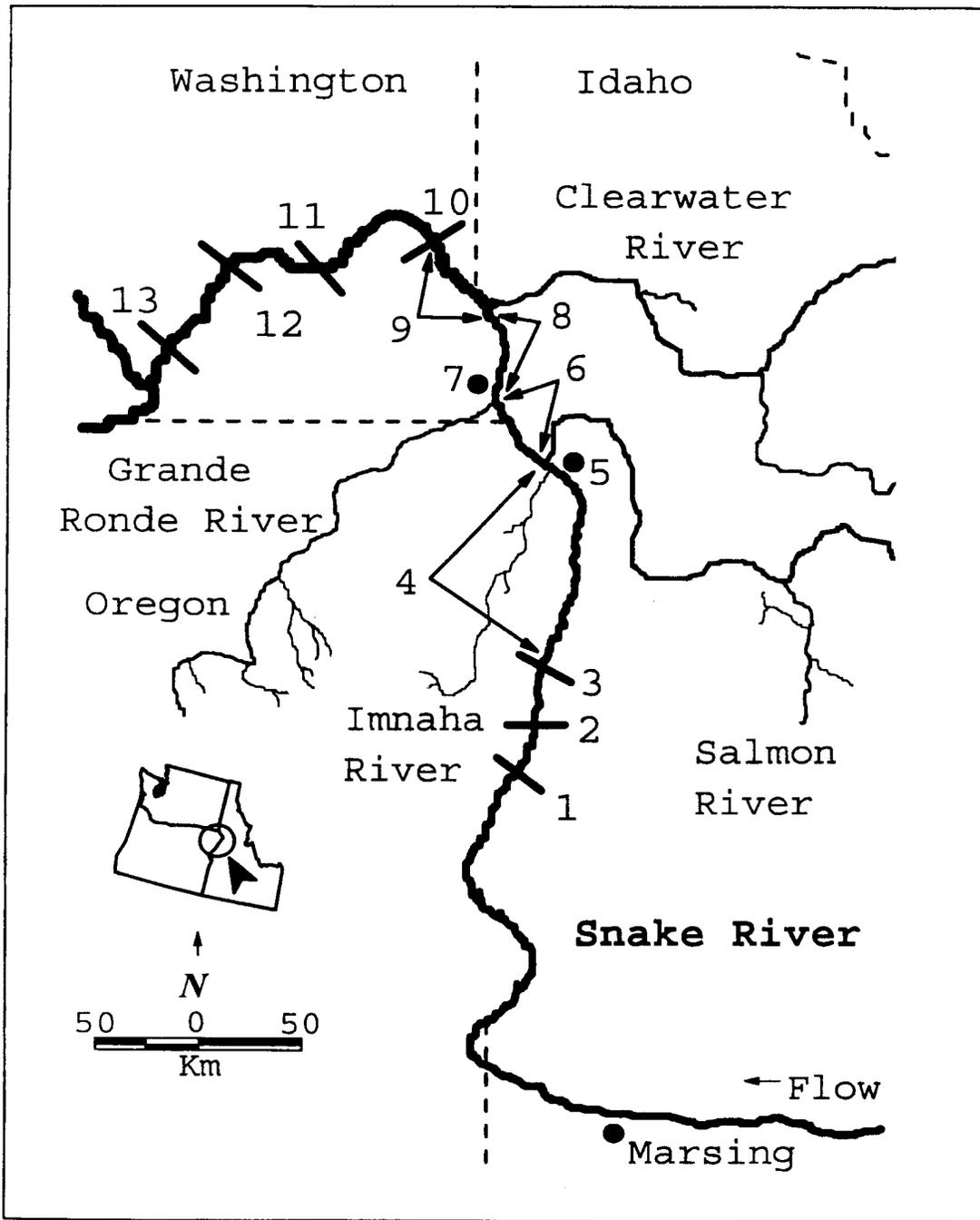


Figure 1. The Snake River including the locations of the upper, middle, and lower reaches, and the historic spawning area near Marsing (approximate rkm 685), major tributaries, dams, and U. S. Geological Survey gaging stations. The locations referenced by number are: 1) Brownlee Dam; 2) Oxbow Dam; 3) Hells Canyon Dam; 4) Upper Reach Snake River; 5) Site 311.5; 6) Middle Reach Snake River; 7) Anatone, Washington; 8) Lower Reach Snake River; 9) Lower Granite Reservoir; 10) Lower Granite Dam; 11) Little Goose Dam; 12) Lower Monumental Dam; and 13) Ice Harbor Dam.

of the proposed recovery goal (1,250 redds) in light of the redd capacity estimates we generate.

Study Area

For a detailed description of the Snake River, we refer the reader to papers by Groves and Chandler (1999) and Dauble and Geist (2000). The Snake River can be divided into three reaches (Figure 1) based on differences in channel morphology and discharge. The volume of water flowing through the upper reach is controlled by releases of water from the Hells Canyon Dam (Groves and Chandler 1999). The Imnaha, Salmon, and Grande Ronde Rivers (Figure 1) provide additional water to the lower reach of the Snake River and cause natural flow fluctuation during spawning.

Between 1986 and 2000, there were 78 documented spawning sites in the upper reach, 11 in the middle reach, and 28 in the lower reach (Garcia et al. 2001). Spawning sites were defined as areas where redds occurred within a relatively contiguous patch of medium gravel to small cobble (long-axis diameter 2.6 to 15.0 cm; Groves and Chandler 1999).

Methods

Study Sites and Maps

From 1991 to 1994, we selected five known spawning sites for study in the upper reach and seven in the lower reach. We did not select any study sites in the middle reach because of low spawner use from 1991 to 1994. We established one primary transect (Figure 2) at 11 of our study sites to represent the habitat used by fall chinook salmon spawners. Three primary transects were established at the largest and most complex study site at river km (rkm) 266.5. The locations of the 14 primary transects were surveyed using an electronic total station.

We also established numerous supplemental transects at approximately 15-m intervals upstream and downstream of primary transects to bound the spawning habitat. We used an 8 mm video camera positioned 1.2 m above the ground to record substrate above the water line along each primary and supplemental transect. Mean long-axis diameter of the dominant substrate was assessed visually in water less than 0.6-m deep. We used an underwater video camera to tape substrate images in water >0.6-m deep (Groves and Garcia

1998). At least 20 substrate measurements were made per transect (Geist et al. 2000) and the measurement locations and channel elevations were surveyed using the total station. We determined the mean long-axis diameter of the dominant substrate in each video image (Groves and Chandler 1999).

We made bathymetric maps of each study site (Figure 2) by inputting the substrate measurement and channel elevation locations into AutoCAD® and Softdesk® mapping software. These maps included the distribution of substrate with long-axis diameters ranging from 2.6 to 15.0 cm (hereafter, spawning substrate patches) and the locations of redds we surveyed between 1991 and 1994.

Estimating Spawning Area

We collected velocity calibration data (Bovee and Milhous 1978) at verticals (Figure 2) spaced along the primary transects using U.S. Geological Survey (USGS) gear or an acoustic Doppler current profiler. We surveyed the location of the verticals using the total station so that verticals could be positioned on the bathymetric maps (Figure 2). Velocity calibration data were usually collected during spawning (flow ranges upper reach = 250 to 300 m³/s; lower reach = 290 to 430 m³/s). We also collected stage-discharge data (Bovee and Milhous 1978) over a wide range of flows (upper reach 260 to 1,190 m³/s; lower reach 280 to 1,300 m³/s). All velocity calibration data were collected during periods of stable flow.

We calibrated the hydraulic model IFG-4 (Milhous et al. 1984) to allow the simulation of mean water column velocity at the verticals over the spawning substrate patches at each study site. Velocity adjustment factors were calculated by dividing the simulated flow by the calculated flow to assess model fit. All of the velocity adjustment factors fell in the range of 0.8 to 1.2 indicating IFG-4 fit the data (Bovee and Bartholow 1995). We used stage-discharge regressions developed for the IFG-4 data decks (Milhous et al. 1984) to simulate water depth at the verticals over the spawning substrate patches at each study site. Depth was simulated by subtracting the surveyed channel elevation at each vertical from the predicted water surface elevation.

Estimating Spawning-Area-per-Redd

The IFG-4 model typically represents the stream bed in the form of rectangles called "cells"

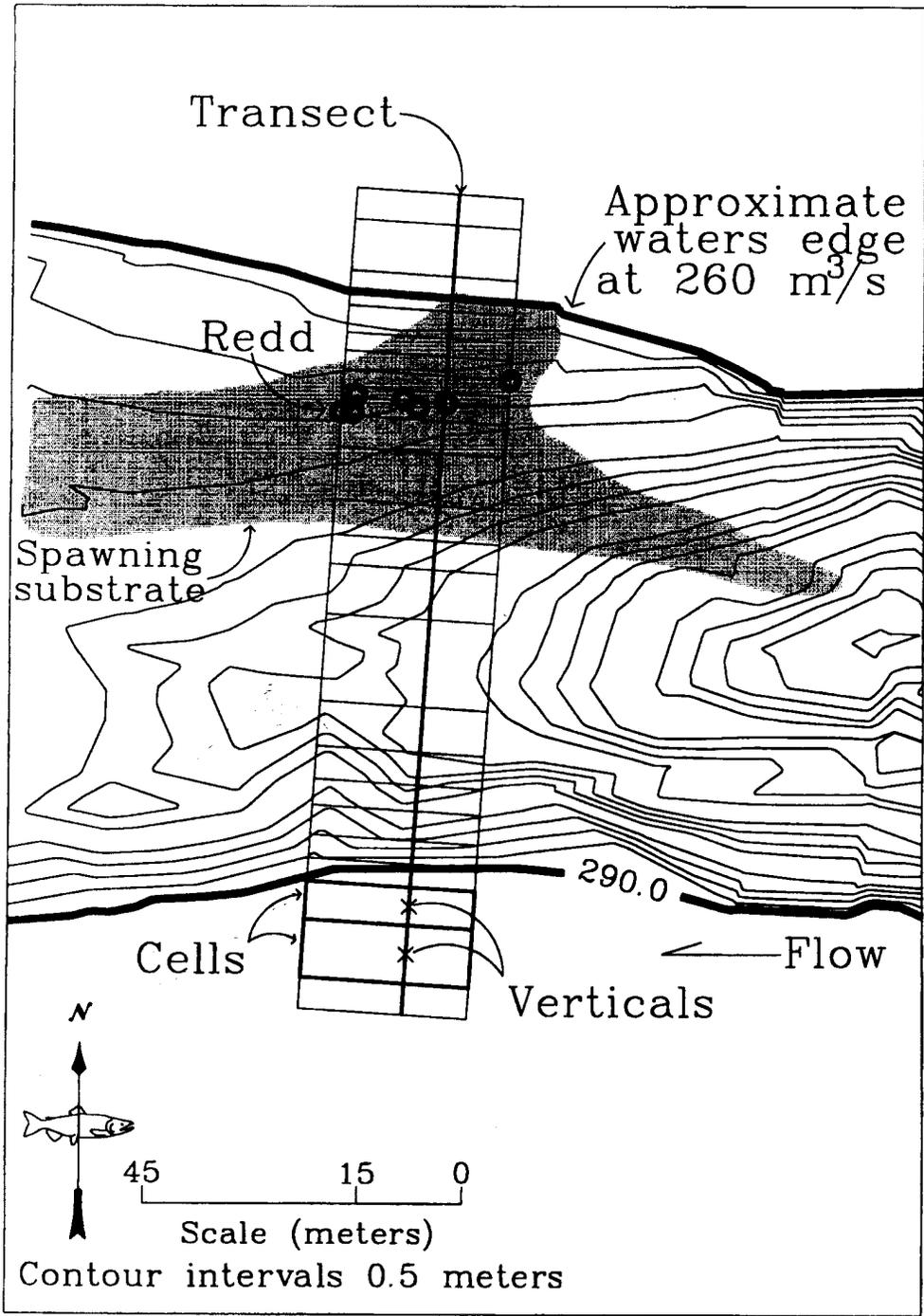


Figure 2. The study site at rkm 311.5 including the location of the spawning substrate patch, primary transect, verticals, cell boundaries, and fall chinook salmon redds.

(Milhouse et al. 1984). We used vertical spacing to determine the width of each cell (Figure 2). We determined cell length two ways. For 11 of the primary transects we based cell length on the maximum distance redds were located up and downstream of the transect (Figure 2). We surveyed one or two redds at the primary transects representing three of our upstream sites, although the substrate patches at these sites were obviously large enough to support additional spawning. We determined cell length at these three sites by using the bathymetric maps to determine the up and downstream distances within the substrate patch that was represented by the primary transect. We then calculated the area of the spawning substrate in each cell by using AutoCAD® and Softdesk® mapping software.

We used IFG-4 and the stage-discharge regressions to simulate water depth and mean column velocity within each cell under the flow that occurred the year we surveyed the maximum number of redds at each study site. We calculated the simulation flow for this analysis as the average of the daily mean flows between the onset and end of spawning. Daily mean flow records for all simulations were obtained from USGS gages at Hells Canyon Dam (rkm 398.6) in the upper reach and Anatone, Washington (rkm 269.7) in the lower reach (Figure 1).

The cells with spawning substrate were considered to be suitable for spawning if the simulated depths ranged from 0.2 to 6.5 m, and the simulated mean water column velocities ranged from 0.4 to 2.1 m/s (Groves and Chandler 1999). We calculated spawning area (m²) for each study site by summing the area of spawning substrate in the cells that met the above suitability criteria for water depth and water velocity. We then estimated spawning-area-per-redd at each study site by dividing spawning area by the maximum observed redd count.

Estimating Redd Capacity

We simulated water depth and mean water column velocity for sites in the upper reach of the Snake River under the stable flow regime (i.e., 260 m³/s). To account for flow fluctuation caused by tributary inflow in the lower reach, we simulated water depth and mean water column velocity at flows of 280, 400, and 520 m³/s. This range included the minimum and maximum daily mean

flows observed in the lower reach during our study. We estimated redd capacity for each site at each simulation flow by dividing spawning area by the minimum value of spawning-area-per-redd calculated as described in the previous section of methods. Finally, we estimated redd capacity with a 95% confidence interval for all 106 known spawning sites in the upper and lower reaches by inputting the redd capacity estimates of the 12 study sites into the equation for a stratified random sample (Krebs 1999).

Results

Spawning area estimates for the 12 study Snake River sites ranged from 601 to 13,239 m² the year the maximum number of redds was surveyed at each study site (Table 1). Spawning-area-per-redd ranged from 70 to 683 m² (Table 1). We selected 70 m² as the area required by spawners to construct a redd.

Spawning area estimated for the study sites under the stable flow regime ranged from 601 to 1,234 m² in the upper reach, and from 773 to 13,239 m² in the lower reach (Table 2). Redd capacity ranged from 9 to 20 for study sites in the upper reach, and from 11 to 189 for study sites in the lower reach (Table 2). Estimated spawning area and redd capacity increased for the lower reach sites at rkm 245.2 (up 21 redds), rkm 266.5 (up 2 redds), rkm 267.8 (up 5 redds), and rkm 267.9 (up 3 redds) as the simulation flow increased from 280 to 520 m³/s (Table 2).

The information required for estimating the redd capacity of the 106 known spawning sites in the upper (n = 78) and lower (n = 28) reaches of the Snake River is given in Table 2. The three estimates of redd capacity were 2,446±1,439 (upper reach flow = 260 m³/s; lower reach flow = 280 m³/s), 2,558±1,427 (upper reach flow = 260 m³/s; lower reach flow = 400 m³/s), and 2,570±1,421 (upper reach flow = 260 m³/s; lower reach flow = 520 m³/s).

Discussion

Assumptions and Limitations

We assumed that redd capacity increases as spawning area increases. A correlation analysis between spawning area and maximum redd count would test this assumption. Gallagher and Gard (1999)

TABLE 1. Estimates of spawning area (SA) per redd (SA/redd) for 12 fall chinook salmon spawning sites along the upper and lower reaches of the Snake River based on the flow (m³/s) during spawning the year the maximum number of redds were counted at each site.

Site (rkm)	Year	Simulation flow (m ³ /s)	SA (m ²)	Maximum redd count	SA per redd (m ²)
Upper reach					
311.5	1992	261	662	5	132
311.7	1993	270	601	1	601
312.3	1994	262	1,234	5	247
349.6	1993	270	1,366	2	683
352.8	1994	262	665	2	333
Lower reach					
245.2	1992	380	3,077	7	440
259.0	1993	411	773	11	70
261.3	1991	465	4,977	20	249
266.5	1993	411	13,239	30	441
267.0	1993	411	1,735	4	434
267.8	1993	411	1,412	6	235
267.9	1993	411	1,262	14	90

TABLE 2. Estimates of redd capacity for 12 fall chinook salmon spawning sites along the upper and lower reaches of the Snake River based a stable flow of 260 m³/s in the upper reach, and a range of flows in the lower reach of 280, 400, and 520 m³/s. The statistics for estimating total redd capacity for the 106 known spawning sites in the upper (n = 78) and lower reaches (n = 28) are also given.

Site (rkm)	Spawning area (m ²) by flow (m ³ /s)				Redd capacity by flow (m ³ /s)			
	260	280	400	520	260	280	400	520
Upper reach								
311.5	662	—	—	—	9	—	—	—
311.7	601	—	—	—	8	—	—	—
312.3	1,234	—	—	—	18	—	—	—
349.6	1,142	—	—	—	20	—	—	—
352.8	664	—	—	—	10	—	—	—
n					5			
Sample mean					13.2			
Sample variance					28.7			
Lower reach								
245.2	—	1,876	3,387	3,387	—	27	48	48
259.0	—	773	773	773	—	11	11	11
261.3	—	4,977	4,977	4,977	—	71	71	71
266.5	—	13,105	13,239	13,239	—	187	189	189
267.0	—	1,735	1,735	1,735	—	25	25	25
267.8	—	1,067	1,412	1,412	—	15	20	20
267.9	—	1,262	1,262	1,475	—	18	18	21
n						7	7	7
Sample mean						50.6	54.7	55.0
Sample variance						4,022.0	3,948.3	5,913.0

reported a significant correlation between chinook salmon spawner density and an estimate of spawning area called weighted usable area (Bovee 1982). We did not conduct a correlation analysis because

spawner number was critically low, thus the majority of the study sites was under utilized. Fall chinook salmon redds counted during aerial surveys increased from 41 in 1991 to 255 in 2000

(Garcia et al. 2001). We may have an opportunity to validate our redd capacity estimates if adult fall chinook salmon escapement to the Snake River continues to increase.

We equated the recovery goal of 2,500 adults to the Snake River spawning grounds to a redd capacity of 1,250 assuming an equal sex ratio. The information on the sex ratio of wild Snake River fall chinook salmon spawners was inadequate for our modeling because it is limited to small samples of carcasses collected haphazardly during spawning surveys. However, the Washington Department of Fish and Wildlife propagates hatchery Snake River fall chinook that are phenotypically and genetically similar to wild fish (Bugert et al. 1995, Marshall et al. 2000). The sex ratio observed for spawners at this hatchery between 1988 and 1996 averaged 0.7 females to 1.0 males (Mendel et al. 1992, 1996). We used a 1.0 to 1.0 ratio to simplify our analysis, and to add a measure of conservatism to our redd capacity estimates.

We expanded the measurements taken at 12 spawning sites to all 106 spawning sites, thereby assuming that redd capacity of study sites represented redd capacity of non-study sites. We sampled approximately 10% of the known spawning sites, which we believe represented the spawning habitat at non-study sites. However, redd capacity within study sites was variable as shown by the relatively wide 95% confidence intervals on our redd capacity estimates. We recommend studying additional sites if future research opportunities become available.

We did not measure factors affecting redd capacity such as inter-gravel flow (Burner 1951, Geist and Dauble 1998, Geist 2000), substrate movement, or substrate recruitment. We assumed that inter-gravel flow would not limit redd capacity or cause variability in redd capacity between sites with the same amount of modeled spawning area. We also assumed that substrate movement and recruitment were in dynamic equilibrium. These are strong assumptions that should be tested in the future at both the spatial and temporal scales.

We did not report redd capacity estimates for extreme flow conditions because data were not available to fit the stage-discharge regression required to run IFG-4. Within the range of flows modeled, we found that redd capacity decreased moderately in the lower reach of the Snake River

as flow decreased. This suggests that the amount of spawning area might limit redd construction at some low flow level, which in turn could have a temporal effect on production by reducing the number of returning spawners 4 to 5 yr later. Stage-discharge data collection under drought conditions would increase modeling opportunities, thereby providing a better understanding of how low flow affects redd capacity.

Redd Capacity

We reviewed the literature at the onset of our study to understand the problems others have encountered when estimating redd capacity. To our knowledge there are no peer-reviewed papers on this topic. Bjornn and Reiser (1991) reviewed unpublished data that clearly showed the potential for overestimating redd capacity when spawning area was based solely on spawning substrate availability. They concluded that redd capacity depended on: the amount of suitable spawning substrate covered by water with acceptable depths and velocities for spawning (i.e., spawning area), and on the area required for a pair of spawning fish (i.e., spawning-area-per-redd).

We modified the Instream Flow Incremental Methodology (Bovee 1982) to estimate spawning area. Although widely applied by biologists, this method can grossly overestimate spawning area (Shrivell 1989). Using Shrivell (1989) for guidance, we made conservative estimates of spawning area by: 1) studying sites known to be used by spawners; 2) calculating spawning area based on the actual shape of the wetted spawning substrate patch rather than the rectangular shape of cells; and, 3) determining cell length using the location of redds or short stretches of habitat with relatively homogenous depths, velocities, substrate, and channel contours.

We used a relatively large value for spawning-area-per-redd (i.e., 70 m²) that was based on the highest redd density we observed. The space required for redd construction probably varies in response to stream size, spawn timing, and spawner density. For comparison, Swan (1989) reported spatial requirements ranging from 21.7 to 75.2 m²/redd. Burner (1951) proposed that female fall chinook salmon require four times the area of a redd to spawn, which equates to 68 m² using the redd surface area of 17 m² reported by Chapman et al. (1986). Using 70 m² added an additional

measure of conservatism to our estimates of redd capacity.

We developed our method for estimating redd capacity to accomplish two objectives. The results obtained for the first objective indicate that redd capacity for the upper and lower reaches of the Snake River ranges from 2,466 to 2,570 under the stable flow regime. The actual carrying capacity of the Snake River for fall chinook salmon redds (or the "best estimate") might be higher because our method was conservative. For example, the estimates of redd capacity would have ranged from 7,875 to 8,283 if we divided spawning area by the 21.7 m² per redd reported by Swan (1989) instead of 70 m².

Management Implications

In light of our redd capacity estimates, we believe that the Snake River can support the 1,250 redds needed to remove Snake River fall chinook salmon from the list of federally protected species. The lowest of the three estimates, 2,466, is roughly twice the de-listing criteria of 1,250 redds. We acknowledge that the 95% lower confidence limits on our redd capacity estimates show that

redd capacity could be as low as 1,007 to 1,149. A stock-recruitment analysis (Ricker 1975) conducted with empirical data collected as spawner escapement increases will be the only way to confirm redd capacity, and to determine if the recovery goal is achievable. Other recovery measures such as spawning gravel enhancement might be necessary if recruitment efficiency is affected by density dependent factors before the recovery goal is attained.

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Literature Cited

- Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society Special Publication 19:83-138.
- Bovee, K. D. 1982. A guide to stream habitat analysis using the Instream Flow Incremental Methodology. Instream Flow Paper 12. U. S. Fish and Wildlife Service, Office of Biological Services. FWS/OBS-82/26.
- Bovee, K. D., and R. Mithous. 1978. Hydraulic simulation in instream flow studies: Theory and techniques. U. S. Fish and Wildlife Service, Instream Flow Group Information Paper Number 5, Fort Collins, Colorado.
- Bovee, K. D., and Bartholow, J. M. 1995. IFIM phase III study implementation. Pages 191-255 In K. D. Bovee (editor). A Comprehensive Review of the Instream Flow Incremental Methodology. U. S. Geological Survey, National Biological Service, Fort Collins, Colorado.
- Bugert R., C. W. Hopley, C. Busack, and G. Mendel. 1995. Maintenance of stock integrity in Snake River fall chinook salmon. American Fisheries Society Symposium 15:267-276.
- Burner, C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fishery Bulletin 52:95-110.
- Chapman, D. W., D. E. Weitkamp, T. L. Welsh, M. B. Dell, and T. H. Schadt. 1986. Effects of river flow on the distribution of chinook salmon redds. Transactions of the American Fisheries Society 115:537-547.
- Dauble, D. D., and D. R. Geist. 2000. Comparison of mainstem spawning habitats for two populations of fall chinook salmon in the Columbia River Basin. Regulated Rivers: Research and Management 16:345-361.
- Gallagher, S. P., and M. F. Gard. 1999. Relationship between chinook salmon (*Oncorhynchus tshawytscha*) redd densities and PHABSIM-predicted habitat in the Merced and Lower American Rivers, California. Canadian Journal of Fisheries and Aquatic Sciences 56:570-577.
- Garcia, A. P., R. D. Waitt, C. A. Larsen, D. Burum, B. D. Arnsberg, M. Key, and P. A. Groves. 2001. Fall chinook salmon spawning ground surveys in the Snake River basin upriver of Lower Granite Dam, 2000. Unpublished report on file at U. S. Fish and Wildlife Service, Idaho Fishery Resource Office, Ahsahka, Idaho.
- Geist, D. R. 2000. Hyporheic discharge of river water into fall chinook salmon (*Oncorhynchus tshawytscha*) spawning areas in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1647-1656.
- Geist, D. R., and D. D. Dauble. 1998. Redd site selection and spawning habitat use by fall chinook salmon: The importance of geomorphic features in large rivers. Environmental Management 22:655-669.
- Geist, D. R., J. Jones, C. J. Murray, and D. D. Dauble. 2000. Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat use in the Hanford Reach, Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 57:1636-1646.

- Groves, P. A., and A. P. Garcia. 1998. Two carriers used to suspend an underwater camera from a boat. *North American Journal of Fisheries Management* 18:1004-1007.
- Groves, P. A., and J. A. Chandler. 1999. Spawning habitat used by fall chinook salmon in the Snake River. *North American Journal of Fisheries Management* 19:912-922.
- Kondolf, G. M., J. C. Vick, and T. M. Ramirez. 1996. Salmon spawning habitat rehabilitation on the Merced River, California; an evaluation of project planning and performance. *Transactions of the American Fisheries Society* 125:899-912.
- Krebs, C. J. 1999. *Ecological Methodology* (2nd edition). Addison-Wesley Educational Publishers, Incorporated. Menlo Park, California.
- Marshall, A. R., H. L. Blankenship, and W. P. Connor. 2000. Genetic characterization of naturally spawned Snake River fall-run chinook salmon. *Transactions of the American Fisheries Society* 129:680-698.
- Mendel, G., D. Milks, R. Bugert, and K. Petersen. 1992. Upstream passage and spawning of fall chinook salmon in the Snake River, 1991. Unpublished report on file at Washington Department of Fish and Wildlife, Snake River Lab, Dayton, Washington.
- Mendel, G., J. Bumgarner, D. Milks, L. Ross, J. Dedloff. 1996. Lyons Ferry Hatchery Evaluation: Fall Chinook Salmon. Unpublished report on file at Washington Department of Fish and Wildlife, Snake River Lab, Dayton, Washington.
- Milhous, R. T., D. L. Wegner, and T. W. Waddle. 1984. User's guide to the physical habitat simulation system. Instream flow information paper Number 11. U.S. Fish and Wildlife Service FWS/OBS-81/43.
- National Marine Fisheries Service. 1992. Threatened status for Snake River spring/summer chinook salmon, threatened status for Snake River fall chinook salmon. *Federal Register* 57:78(22 April 1992):14,653-14,663.
- National Marine Fisheries Service. 1995. Proposed recovery plan for Snake River salmon. Unpublished report on file at U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, Portland, Oregon.
- Ricker, W. E. 1975. Computation and Interpretation of Biological Statistics. *Bulletin 191 of the Fisheries Research Board of Canada*. Ottawa, Ontario.
- Shrivell, C. S. 1989. Ability of PHABSIM to predict chinook salmon spawning habitat. *Regulated Rivers: Research and Management* 3:277-289.
- Swan, G. A. 1989. Chinook salmon spawning surveys in deep waters of a large regulated river. *Regulated Rivers: Research and Management* 4:355-370.
- Wunderluch, R. C., B. D. Winter, and J. H. Meyer. 1994. Restoration of the Elwha River ecosystem. *Fisheries* 19:11-19.

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