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IDAHO COOPERATIVE FISH AND WILDLIFE RESEARCH UNIT

MIGRATION DEPTHS OF ADULT STEELHEAD IN THE LOWER COLUMBIA AND SNAKE RIVERS IN RELATION TO DISSOLVED GAS EXPOSURE, 2000

Report for project ADS-00-5

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Preface

Most historical studies that have addressed effects of dissolved gas exposure on development of gas bubble disease (GBD), reproductive potential, and fish survival have been conducted in a laboratory setting. An important question yet to be answered is the applicability of using those laboratory results to evaluate in-river conditions experienced by aquatic organisms since depth distribution influences the biological effects of total dissolved gas supersaturation. In this report we provide information on the in-situ depths of migration for adult steelhead migrating through the lower Columbia and Snake rivers in relation to the degree of exposure to and avoidance of gas supersaturated water. Study objectives relate to RPA's 24, 107, and 115 in Section 9.6.1 of the "Hydrosystem" Biological Option (NMFS 2000).

Acknowledgements

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Abstract

High spill volume at dams can create supersaturated dissolved gas conditions that may have negative effects on fishes. Water spilling over Columbia and Snake River dams during the spring and summer freshet creates plumes of high dissolved gas that extend downstream of dam spillways and creates gas supersaturated conditions that do not equilibrate in reservoirs. During 2000, 201-adult steelhead *Oncorhynchus mykiss* were tagged at Bonneville Dam with archival radio data storage transmitters (RDSTs) that recorded depth and water temperature as they migrated through tailraces and reservoirs of lower Columbia and Snake River dams. Migration depth plays a central role in the development and expression of gas bubble disease because hydrostatic compensation reduces the effects of exposure at greater depths. Swimming depths from 115 of the 201 adult steelhead tagged with RDSTs were used to estimate the degree of exposure to various dissolved gas conditions in the lower Columbia and Snake rivers. Migration paths of 28 individual fish tagged with RDSTs were monitored in the tailraces of Bonneville and Ice Harbor dams and combined with output from a two-dimensional dissolved gas model to estimate the degree of uncompensated dissolved gas exposure.

We found that adult steelhead, like Chinook salmon, spent a majority of their time at depths deeper than 2 m, providing at least 20% hydrostatic compensation, interspersed with periods lasting minutes at depths shallower than 2 m. The longest successive time an individual fish was observed shallower than 1 and 2 m was 17 h and 8.5 d, respectively. Steelhead spending the longest durations of time near the surface (< 2 m) were likely near the mouth of a Columbia River tributary based on body temperatures obtained from RDST data that were cooler than the mainstem Columbia River.

Depth uncompensated exposure based on model results was estimated to be 7.1% of the time in the Bonneville tailrace and 0% of the time spent in the Ice Harbor tailrace. Most (87%) of the uncompensated exposure was less than 115% total dissolved gas supersaturation (TDGS) which is considered a conservative level of exposure known to cause gas bubble disease (GBD) and mortality. Adult steelhead tended to migrate near the shoreline with approximately equal proportions of fish entering or leaving areas of the river with elevated dissolved gas levels. No significant association existed between

crossing the river and the position of the dissolved gas plume downstream of Bonneville Dam.

Although degree of dissolved gas exposure was not considered lethal, dams could be operated during periods of potential high levels to direct water away from shorelines to minimize the potential for encountering water with high TDGS levels. Additional research is needed to confirm the effects of short but frequent exposure to supersaturated dissolved gas conditions on reproductive potential and survival.

Introduction

Gas bubble disease (GBD) is a condition that can affect fish and aquatic invertebrates residing in water that has become supersaturated with atmospheric gases as a result of either natural phenomena (photosynthesis, waterfall) or human activity (hydroelectric projects). Within the Columbia River Basin supersaturated conditions routinely occur in the lower Columbia and Snake rivers during the spring and summer and are largely attributed to spilling water over dam spillways. Spilling water at dam spillways has been one management strategy to increase survival of juvenile salmonids *Oncorhynchus spp.* passing Columbia and Snake River dams (Schoeneman et al. 1961; Muir et al. 2001). However, voluntary use of spill poses a potential conflict with the management of adult salmonids because the spill period coincides with the timing of adult and juvenile spring–summer Chinook salmon *O. tshawytscha* and steelhead *O. mykiss* upstream migration. Supersaturated conditions persist through the length of the lower Columbia and Snake rivers and throughout the water column due to a lack of strong turbulence; therefore, not allowing water to equilibrate rapidly with the atmosphere (Ebel, 1969). Adult exposure is most likely to occur in reservoirs, tailraces and near fishway entrances at dams, and less likely inside fishways because adult fish ladders quickly degas supersaturated water (Bouck 1996).

Supersaturated water conditions can cause GBD or gas bubble trauma (GBT) in fish when tissue and fluids of fish exposed to supersaturated water also become saturated (Weitkamp and Katz 1980). Gases can then come out of solution, resulting in bubble formation when the pressures of dissolved gases are in excess of the sum of barometric and hydrostatic pressures (Weitkamp and Katz 1980, Colt 1984), a process that is analogous to "the bends" in human divers. Therefore, the hydrostatic pressure achieved as a result of a fish's depth plays a central role in evaluating the biological effects of total dissolved gas supersaturation (TDGS) on fish. Each meter of depth exerts pressure that increases the solubility of dissolved gas to compensate for approximately 10% of saturation, where 100% represents fully saturated water (Weitkamp and Katz 1980). Consequently, an increase in fish depth provides a rapid and linear decrease in the potential for gas bubble formation (Figure 1). Conversely, fish occupying shallower depths where pressure is insufficient to compensate for supersaturation can develop excessive bubble formation that can cause potentially lethal vascular and cardiac blockage and hemorrhaging. In addition to direct effects, GBT has also been known to increase a fish's susceptibility of disease and predation, in addition to reducing growth and swimming performance (Dawley and Ebel 1975). Maintaining a single depth where adequate hydrostatic compensation is achieved may not be required to avoid GBD. Intermittent periods of hydrostatic compensation through changes in depth of swimming reduced signs of gas bubble disease (Meekin and Turner 1974; Dawley et al. 1975; Weitkamp 1976; and Knittel et al. 1980).

Little is known about the migration depths and behavior of adult steelhead in the lower Columbia and Snake rivers. Our study objectives were 1) to evaluate the depth distribution for adult steelhead in a riverine environment where gas supersaturated water exits, 2) to evaluate associations between the migration depths and migration routes of adult steelhead and the total dissolved gas concentration of the water in the lower Columbia and Snake rivers as a preliminary test of whether fish altered their migration behavior when encountering supersaturated conditions, and 3) to evaluate the degree of depth uncompensated exposure for a sub-sample of fish. The following objectives relate to reasonable and prudent actions 24, 107, and 115 described in section 9.6.1 of the Biological Option (National Marine Fisheries Service 2000).

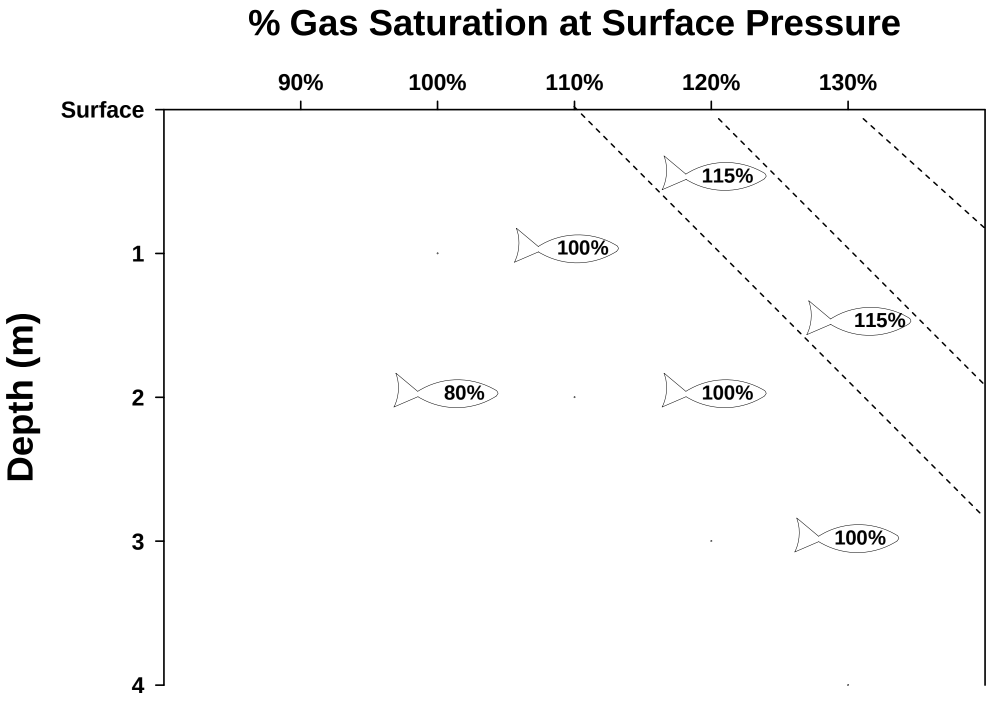


Figure 1. General representation between measured and actual total dissolved gas experienced by fish at various depths in the water column (modified from Weitkamp et al. 2003).

Study Area

Our study area included the lower Columbia River from release sites at river kilometer (rkm) 225.6 (located approximately 10 km below Bonneville Dam) upstream to the Columbia and Snake River confluence (rkm 521.6), and the lower Snake River from the mouth upstream to Lower Granite Dam (rkm 694.6; Figure 2). Mobile tracking efforts were concentrated in two reaches immediately downstream of Bonneville and Ice Harbor dams where horizontal gradients of dissolved gas occur as a result of water spilling over dam spillways. Radio-tagged steelhead were tracked by boat from the Dodson, OR, and Skamania, WA, release sites at (rkm 225.5) upstream approximately 10 km to Bonneville Dam (rkm 235.1). The main channel has depths that are generally greater than 20 m with shallow side channels around two large islands (Romar Books Ltd. 1991). The banks downstream of Bonneville Dam are generally steep and rocky.

The second reach was located on the lower Snake River immediately downstream of Ice Harbor Dam. Radio-tagged fish were tracked from the Snake River mouth (rkm

521.6) upstream to Ice Harbor Dam (rkm 537.7). The width of the Snake River downstream of Ice Harbor Dam varies with location but is generally < 500 m. From the Snake River mouth upstream approximately 8 km to Strawberry Island the shipping channel is located mid-river. Upstream of Strawberry Island the shipping channel parallels the north shoreline. The depth of the shipping channel varies with location but is generally > 6 m (Romer Books Ltd. 1991). Water depths adjacent to the channel are shallower, ranging from 1-3 m depending on dam discharge (Romer Books Ltd. 1991). The north bank in this section of river is steep and rocky, whereas the south bank rises gradually encompassing several small islands.

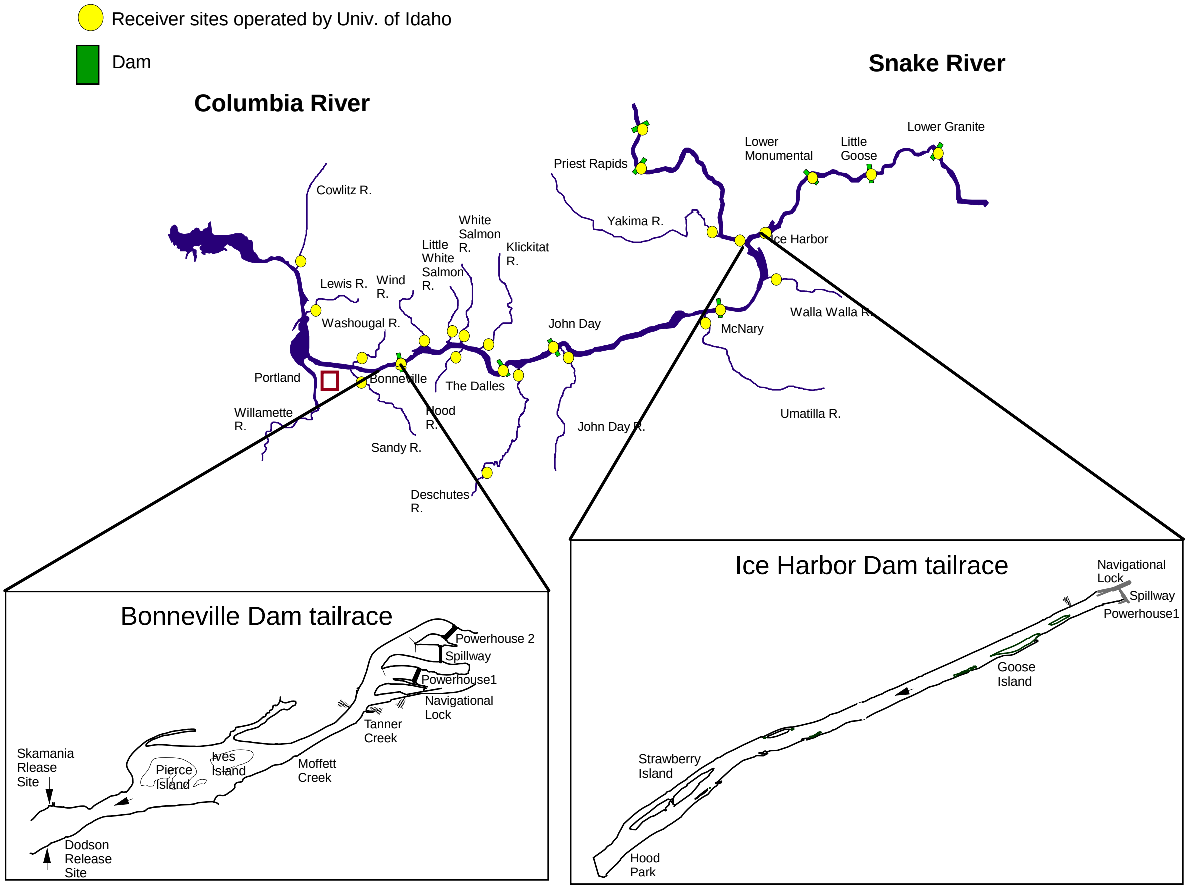


Figure 2. The Columbia and Snake rivers, where the migration of radio-tagged adult steelhead was monitored during 2000 (enlarged areas indicate sections of more intense boat tracking).

Methods

Tagging Procedures

Adult steelhead were trapped and tagged at Bonneville Dam from 1 June through 22 October 2000. A total of 1,155 steelhead were tagged intragastrically with either a 3-V (4.3 ×1.4 cm; 11 g in air), 7-V (8 × 1.6 cm; 29 g in air) standard radio transmitter, or 3-V (9 × 2 cm; 34 g in air) radio data storage (RDST) transmitter. Steelhead were tagged in approximate proportion to the daily fish counts at Bonneville Dam (Figure 3). Radio data storage transmitters were programmed to record temperature at 1-min intervals and pressure at 5-s intervals during upstream migration, which allowed 40 d of data storage. Accuracy of the pressure sensor in the RDST was 0.7 psi (0.5 m) and the accuracy of the temperature sensor was 0.15 °C at water temperatures of 0-20 °C. These transmitters were placed in 201-adult steelhead. Tagged fish were released at two locations downstream from Bonneville Dam, Dodson Landing (rkm 225.6) on the Oregon shore or Skamania Landing (rkm 224.5) on the Washington shore (Figure 2). Radio data storage transmitters were removed from the fish and replaced with a standard radio transmitter at the adult fish trap at Lower Granite Dam to continue monitoring fish migration.

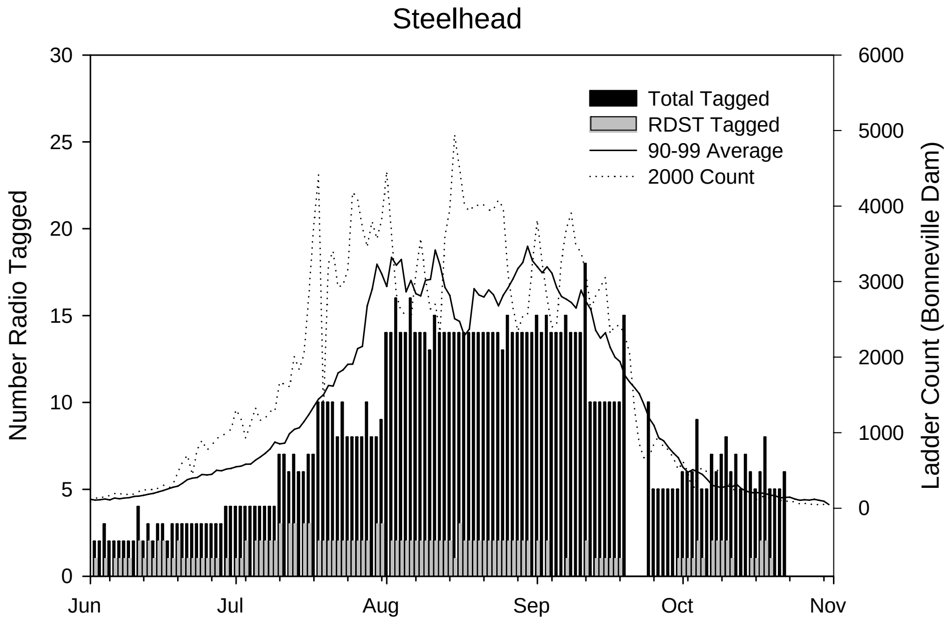


Figure 3. The timing and number of adult steelhead radio-tagged daily at Bonneville Dam in 2000 (dark bars) relative to the ladder counts at Bonneville Dam during 2000 (solid line). The 10-year average (1990-1999) ladder counts for adult steelhead are also shown (broken line).

Fine-scale Evaluation of Dissolved Gas Exposure

Radio-tagged adult steelhead were mobile tracked by boat to evaluate specific locations and migration routes for fish downstream from dams where horizontal gradients of dissolved gas can occur (Scheibe and Richmond 2002). Information regarding migration routes and the depth of migration at specific locations was used in coordination with simulated dissolved gas levels (Richmond et al. 1999) to estimate dissolved gas exposure histories for individual fish (Figure 4).

Individual fish migration routes were determined by using boats equipped with directional antennae and Lotek SRX 400 radio receivers downstream from Bonneville and Ice Harbor dams from June through October. Tagged fish were tracked from release sites to the boat-restricted zone downstream from Bonneville Dam, and from the Snake River confluence to the boat-restricted zone downstream from Ice Harbor Dam. Tracking typically consisted of locating fish every 10-20 min during daylight hours as they moved through tailraces. Tracking preference was given to RDST-tagged fish to determine fish locations needed to estimate degree of exposure to dissolved gas. Transmitter channel and code, location, date, time, and tracking routes were recorded on GIS maps of each area. Logistic regression analysis was used to evaluate associations between release locations, positions of dissolved gas plumes, and fish migration paths.

Logit [pr(Y = 1)] = $\beta_o + \beta_1$(release site) + β_2(gas plume location) + β_3(release site*plume location) where,

Y denotes river crossing status (1 = fish crossed, 2 = fish didn't cross river),
Release site (1 = Dodson, 2 = Skamania), and
Gas plume location = Same side as fish, mid-river, or opposite side as fish.

Output from a two-dimensional fluid dynamics model (MASS2; Richmond et al. 1999) was used to estimate dissolved gas concentrations encountered by 26 steelhead downstream of Bonneville Dam and by 2 steelhead in the Snake River downstream from Ice Harbor Dam. Simulations of flow velocities, water temperature, and gas saturation were run for the time each fish was tracked in the Bonneville and Ice Harbor tailraces. These simulations provided information at approximately 30 m increments during a fish's track (Figure 4) and it was assumed that dissolved gas levels did not vary vertically

(Richmond et al. 1999). Degree of exposure was estimated using the depth of the fish from RDSTs and the compensation depth (depth that provides complete hydrostatic pressure compensation) determined using total dissolved gas pressure estimated from the MASS2 model output where:

Compensation Depth (m) = [(Barometric Pressure mm Hg – TDG Pressure mm Hg) / 23] * 0.3048 (U.S Army Corps of Engineers 1998)

and

Post Compensation Exposure (%) = [(Compensation Depth m – Fish Depth m)]*10 + 100

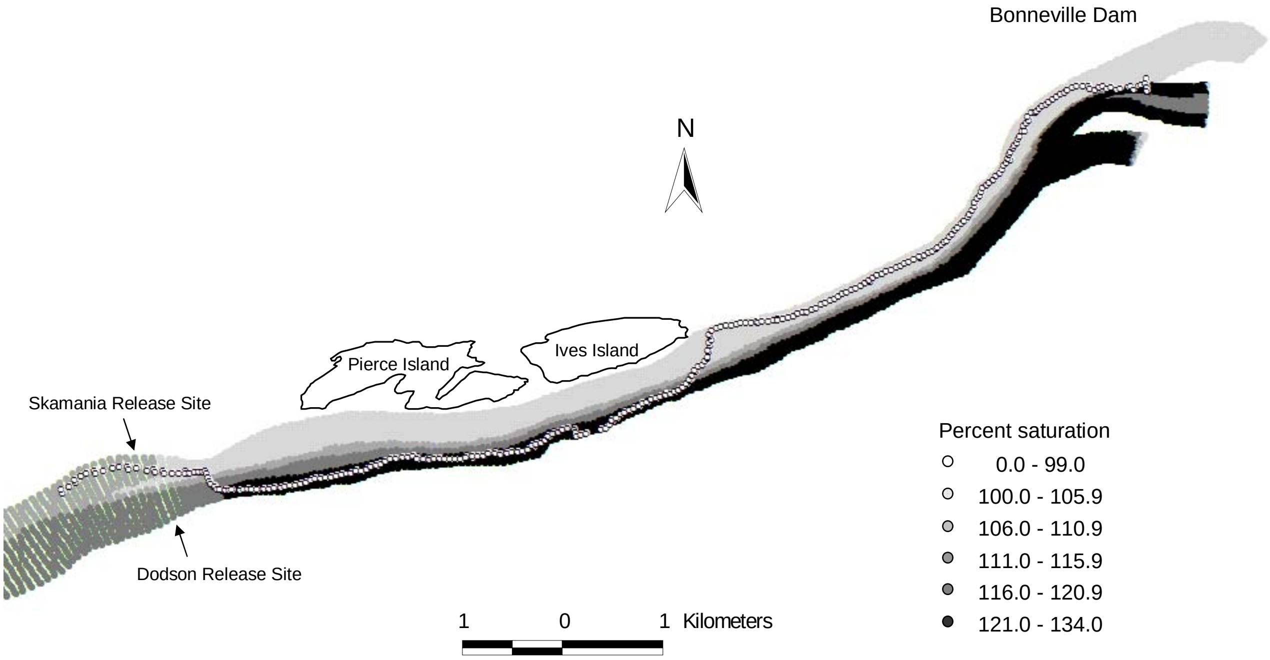


Figure 4. Simulated (MASS2) percent saturation on 24 July 2000 downstream from Bonneville Dam. Circles represent locations for fish (RDST #2435A). The circle shade represents the magnitude of post compensation exposure (percent saturation equivalent to what the fish would experience after taking into consideration hydrostatic compensation).

Large-scale Evaluation of Dissolved Gas Exposure

Steelhead movements past dams, through reservoirs, and into tributaries were determined using fixed radio receivers (radio receivers connected to aerial antennas or underwater antennas) located at all major tributaries and dams in the Columbia and lower Snake rivers (Figure 2). Aerial antennas were used with sequentially scanning receivers (6 s per frequency) while underwater antennas were used in combination with SRX/DSP receivers capable of simultaneously monitoring several radio transmitter frequencies and antennas. The migration history of individual fish was separated into passage segments in reservoirs and in the tailraces of dams. Fish were considered in a tailrace of a dam based on the time period between the last record on directional aerial antennas downstream from each dam (range 0.5 to 3.2 km) and entry into dam fishways based on records from underwater antennas located at fishway entrances, the collection channel or navigation lock (Figure 5). Time spent in monitored tributaries was excluded from this analysis. The Wind, Little White Salmon, White Salmon, Klickitat, Hood, Deschutes, and John Day rivers were continually monitored by fixed receivers; Eagle and Herman creeks were monitored on a weekly basis.

We examined patterns of depth use throughout the migration by calculating the median migration depth of each fish in the Columbia and Snake River reservoirs and tailraces using RDST data. Medians were reported and used in statistical analysis rather than means because depth distributions were asymmetrical and skewed towards deeper depths. Mixed-model, repeated measures ANOVA was used to test for differences in median migration depth of individual fish (=subjects) among reservoir or tailrace locations (fixed effect), and using compound symmetry as the covariance structure. The Kenward-Roger method estimated degrees of freedom, resulting in fractional degrees of freedom. Multiple comparisons of the median migration depth for groups of individuals at each reservoir or dam tailrace were performed using a Tukey type post hoc statistic (Zar 1999). Comparisons of median migration depths for individual fish during spill and no spill conditions at each reservoir were made using a Mann-Whitney test. Degree of exposure to dissolved gas supersaturation was estimated as the percentage of time fish were observed near the surface (between surface and 2 m) and duration of depth uncompensated exposure was determined as the successive depth records shallower than

1 and 2 m. The limited coverage of dissolved gas monitoring stations in the system made it difficult to determine levels of dissolved gas encountered by fish (Figure 6). Therefore, we evaluated the depth of migration that would provide reduction of 10% and 20% total dissolved gas pressure (TDGP) through hydrostatic compensation because this degree of compensation should have prevented bubble formation despite exposure to supersaturated conditions given the degree of supersaturation observed in-river (Figure 7).

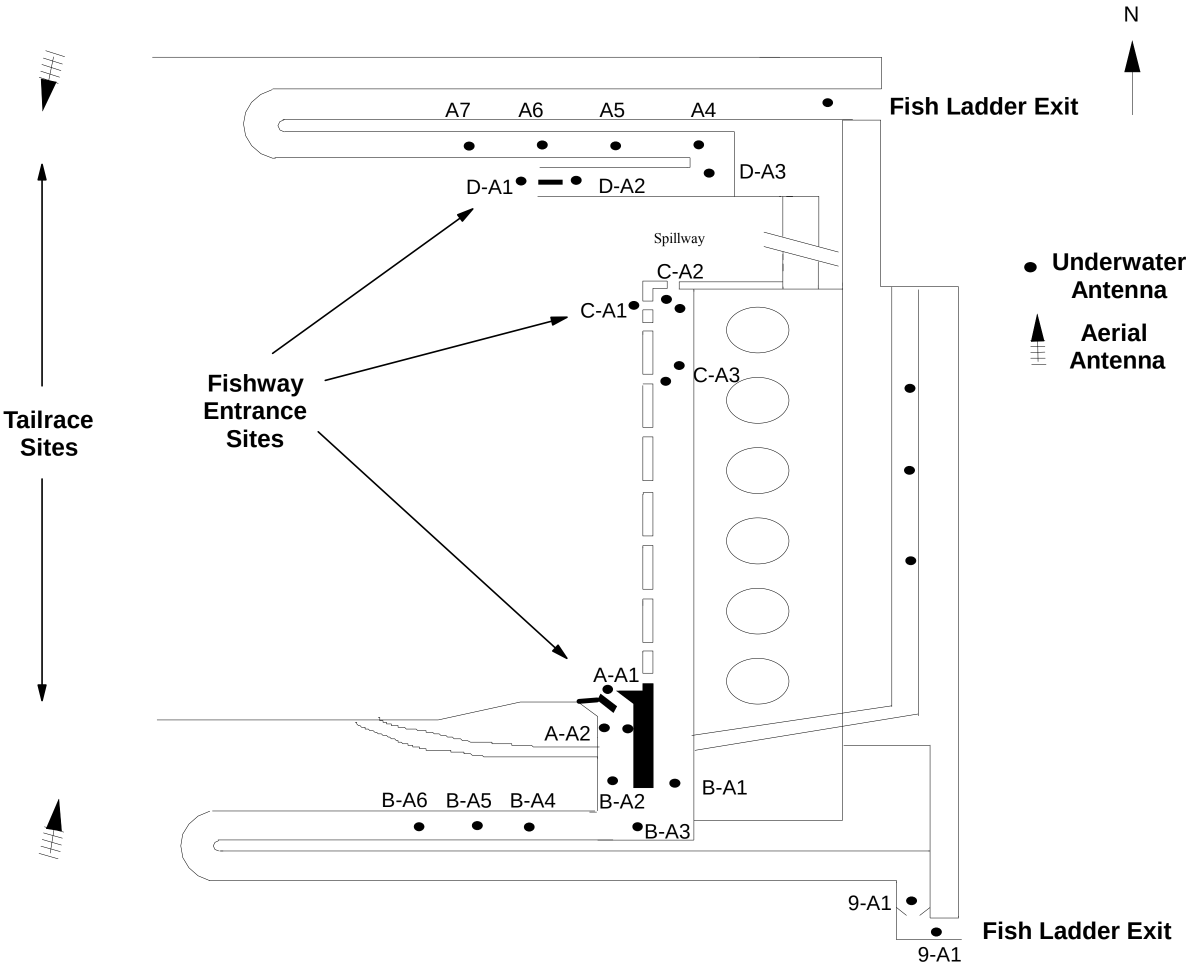


Figure 5. Diagram of Ice Harbor Dam in 2002 with location of aerial tailrace antennas and fixed underwater antennas.

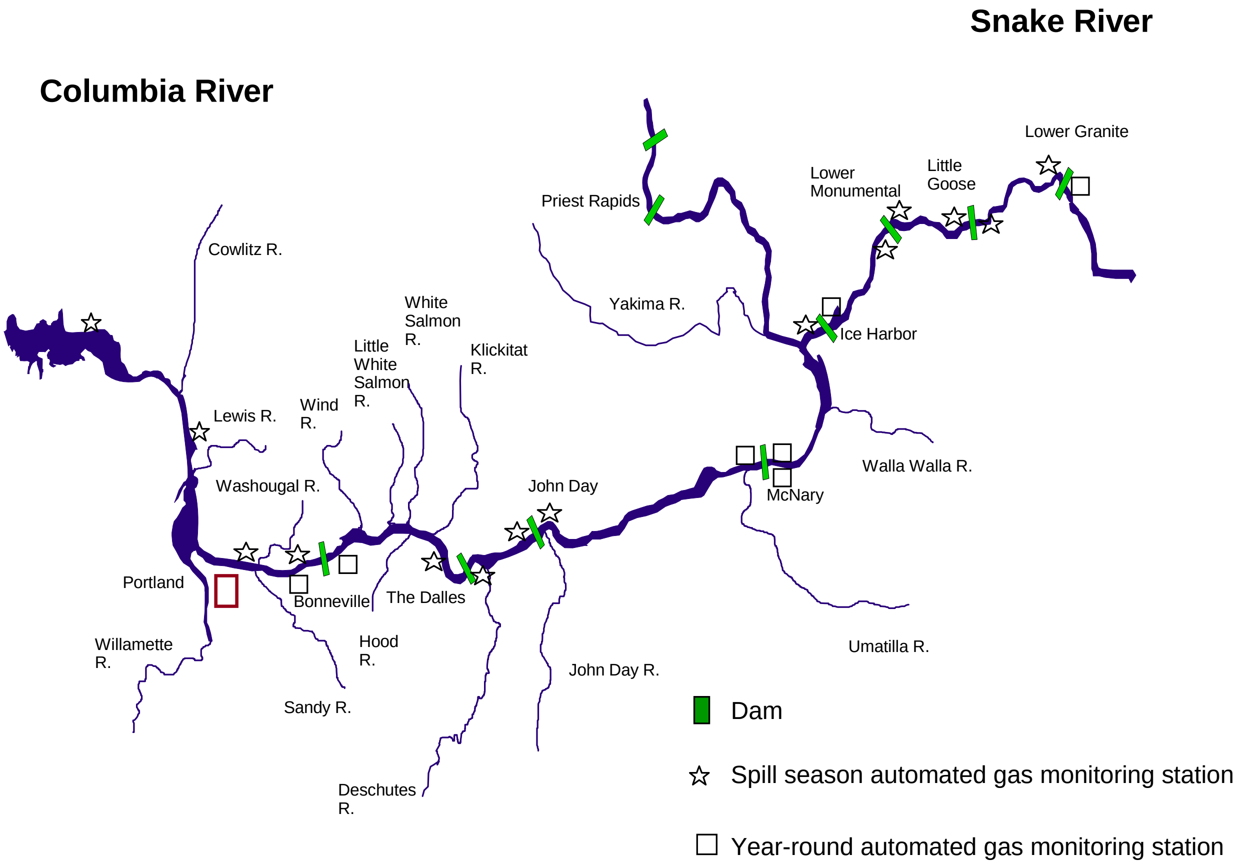


Figure 6. Locations of lower Columbia and Snake River dissolved gas monitoring stations.

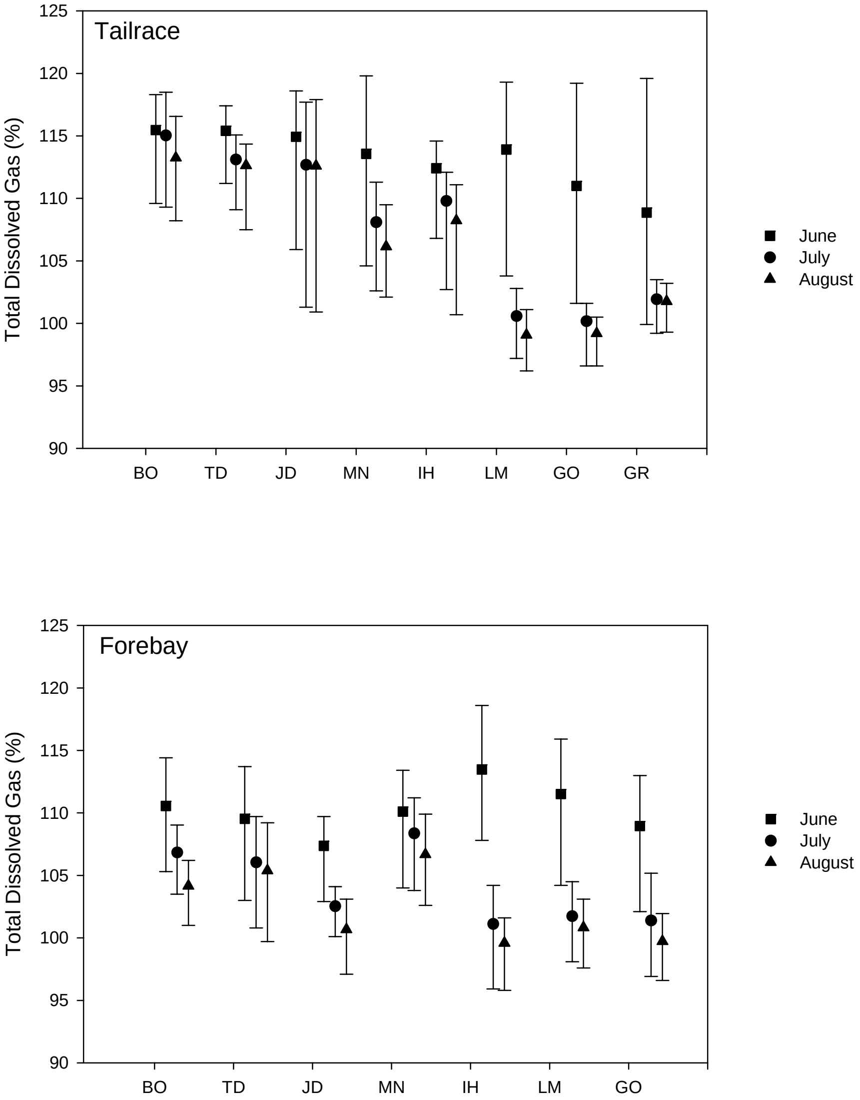


Figure 7. Mean and 90th percentiles of hourly total dissolved gas concentrations (%) in the lower Columbia and Snake River dam tailraces and forbays in June-August of 2000; B0 = Bonneville Dam, TD = The Dalles Dam, MN = McNary Dam, IH = Ice Harbor Dam, LM = Lower Monumental Dam, GO = Little Goose Dam, GR = Lower Granite Dam. Data were downloaded from the U.S. Army Corps of Engineers Technical Management Team internet site (U.S. Army Corps of Engineers 1998).

Results

Fine-scale Evaluation of Dissolved Gas Exposure

Of the 1,155 steelhead released with radio transmitters downstream from Bonneville Dam during the study period, 44 steelhead (combination of RDST and standard transmitters) were tracked sufficiently to summarize migratory routes relative to the position of the dissolved gas plume downstream from Bonneville Dam. Of the tracked steelhead, approximately equal proportions were released on the WA (55%) and OR (45%) shores. Seven steelhead (16% of 44) were monitored migrating when the higher dissolved gas plume was positioned mid-river, a condition that occurs during spill with approximately equal discharge from powerhouse 1 and powerhouse 2 (Appendix Figure 1). Seventeen fish (39%) were tracked when the higher dissolved gas plume was located along the Washington shore which occurs when the majority of discharge is from powerhouse 1 (Figure 8; Appendix Figure 2). Seventeen fish (39%) were tracked with the higher dissolved gas plume along the Oregon shore; with the majority of discharge from powerhouse 2 (Figure 9; Appendix Figure 3). Three fish were tracked when no water was being spilled at Bonneville Dam (Appendix Figure 4).

Adult steelhead typically migrated in close proximity to shorelines (usually within 50 m) with little time spent mid-river except to cross between shorelines. We found neither an association between crossing events and release location (logistic regression, df = 1, *P* = 0.218) nor between crossing events and the location of the dissolved gas plume (logistic regression, df = 1, *P* = 0.484). Steelhead in the Bonneville tailrace tended to cross the river (33 of 44 fish or 75% crossed at least once). We observed a trend where more fish crossed the river into water with elevated gas levels (10 of 44 fish or 23%) than were leaving water with elevated gas levels (5 of 44 fish or 11%). Five steelhead crossed the river into the dissolved gas plume before leaving and 2 steelhead crossed the river, leaving the dissolved gas plume before re-entering. Of the 11 steelhead that did not cross, 6 fish where observed migrating in the dissolved gas plume.

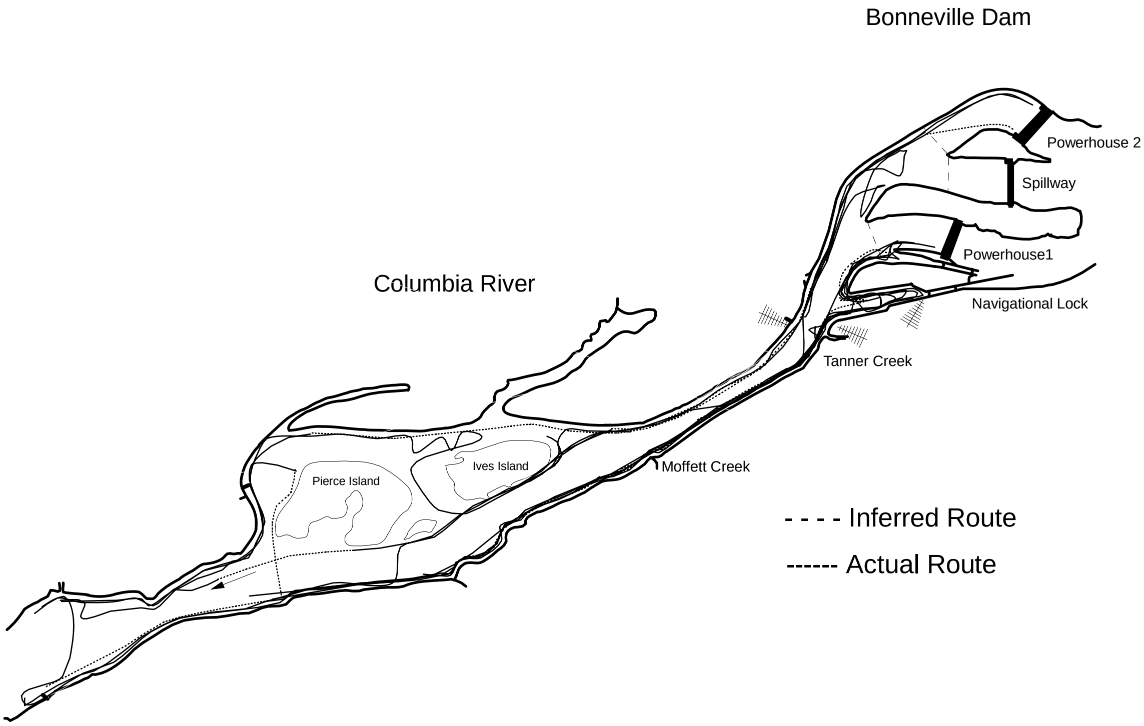


Figure 8. Migration routes of adult steelhead in the Bonneville tailrace during 2000 with spill and discharge from powerhouse 1 (Washington Shore Dissolved Gas Plume).

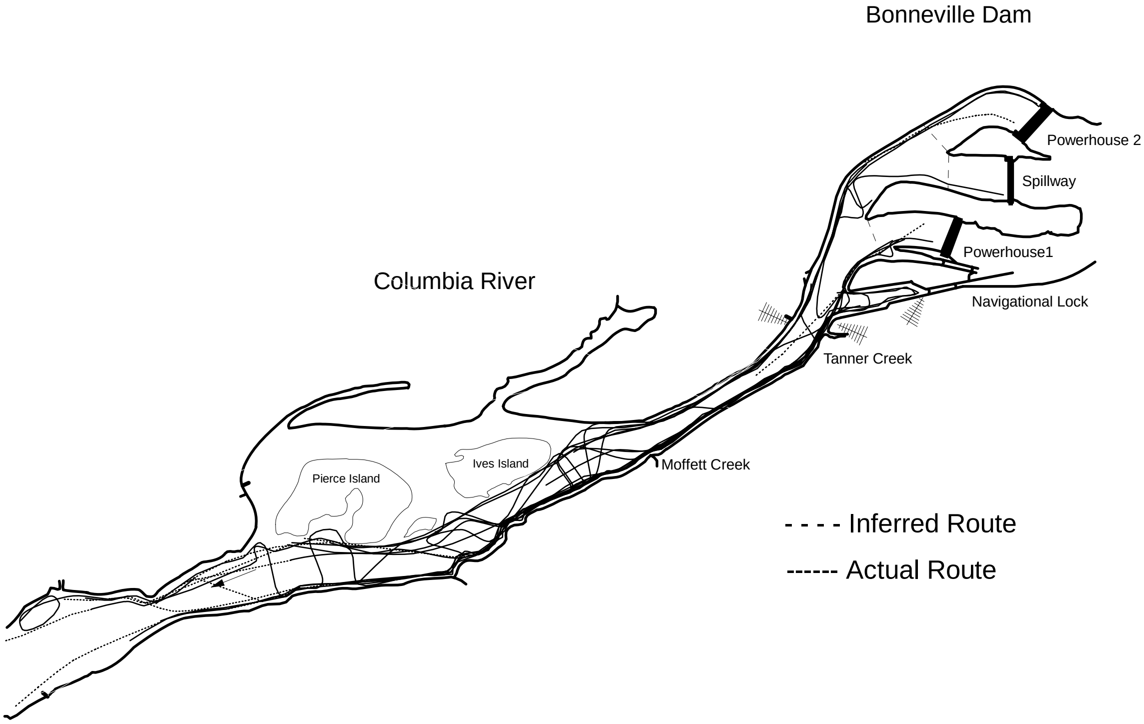


Figure 9. Migration routes of adult steelhead in the Bonneville Dam tailrace during 2000 with spill and discharge from powerhouse 2 (Oregon shore Dissolved Gas Plume).

Thirty steelhead were partially tracked from the confluence of the Snake River to Ice Harbor Dam. Based on model simulations the position of the dissolved gas plume downstream from Ice Harbor Dam changed frequently throughout the day making it unfeasible to accurately determine if fish were avoiding the dissolved gas plume. Migration behavior of fish in the Ice Harbor tailrace was similar to fish downstream from Bonneville Dam with respect to near-shore orientation (Figures 10). However, fish observed migrating downstream of Ice Harbor Dam in late June after water levels dropped showed a strong tendency to migrate up the shipping channel along the north shore (Figure 10).

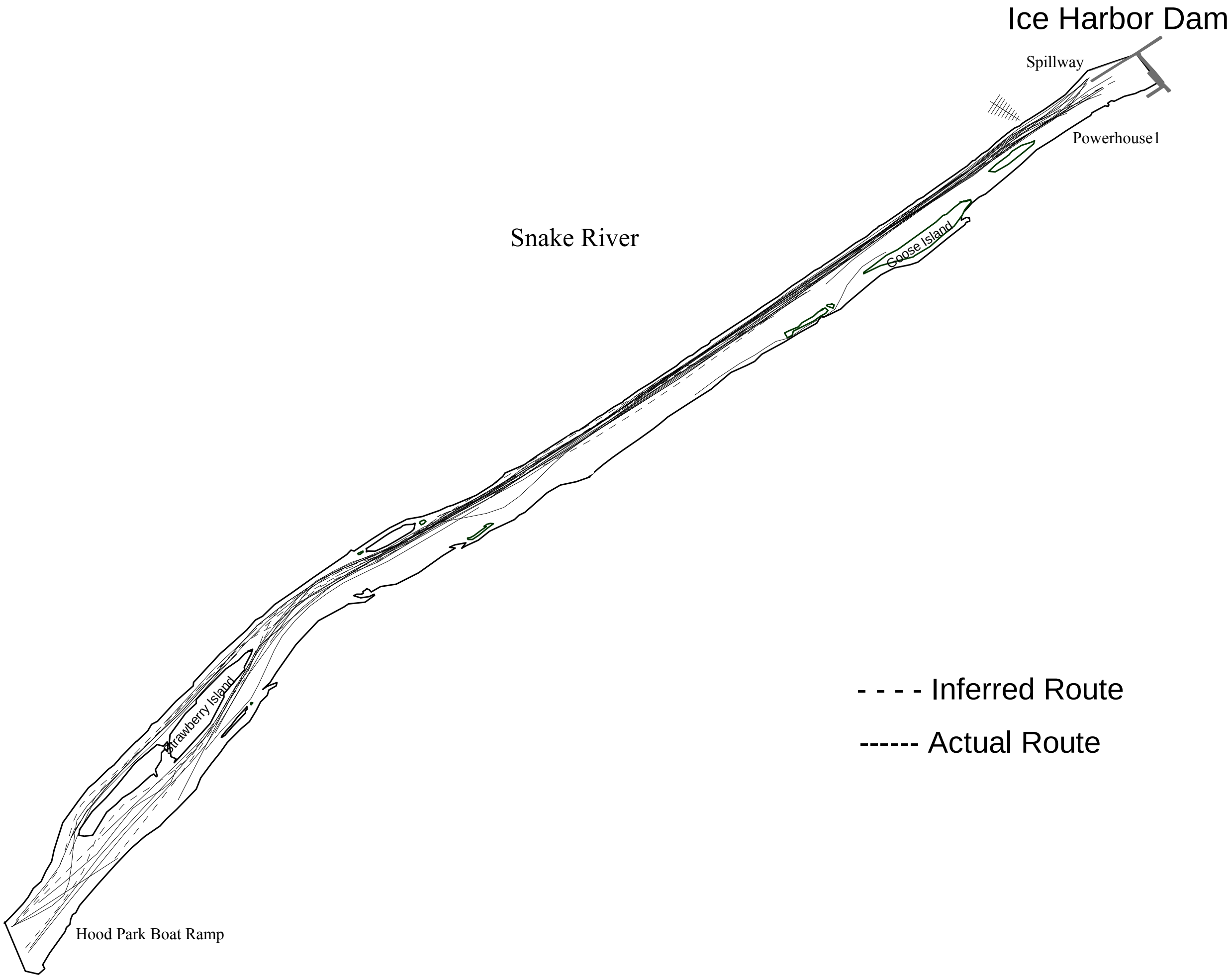


Figure 10. Migration routes of adult steelhead in the Ice Harbor Dam tailrace during 2000.

Archived depth and temperature data were retrieved from 26 steelhead tracked downstream from Bonneville Dam and from 2 steelhead tracked downstream from Ice Harbor Dam. These fish were sufficiently deep in the water column to receive complete hydrostatic compensation 93% of the time spent in the Bonneville tailrace and 100% of the time in the Ice Harbor tailrace based on dissolved gas levels estimated from MASS2 model simulations and corresponding fish locations and depth records (Figure 11); 2.8% of the depth uncompensated exposure was equivalent to a level of TDGS between 101-105%, 1.3% to a level between 106-110%, 2.0% to a level between 111-115%, and 0.9% to a level higher than 115%.

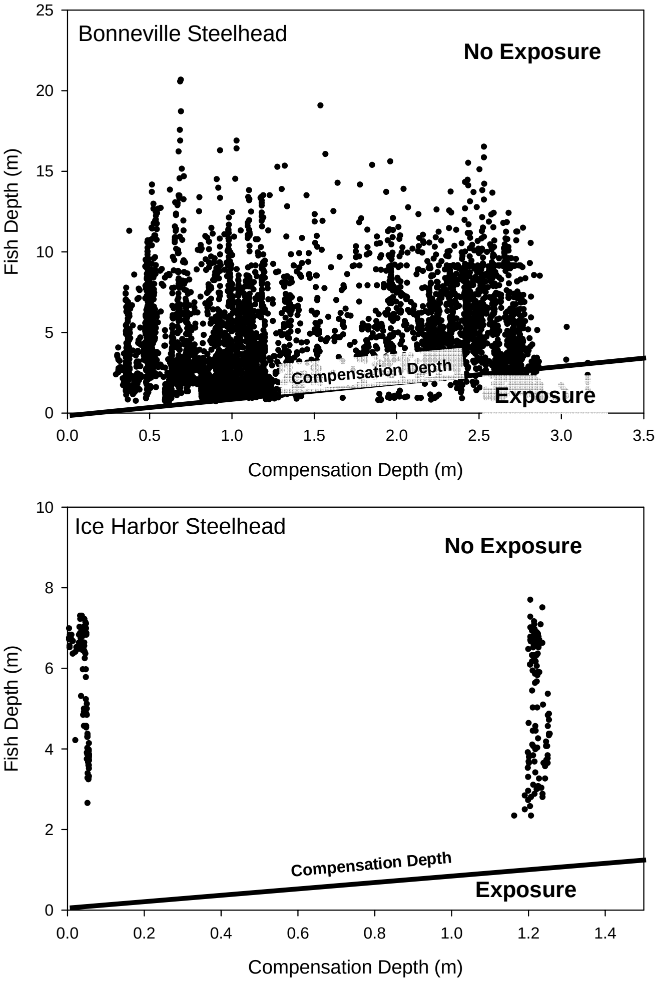


Figure 11. Relationship between the MASS2 modeled compensation depth (depth where there is complete hydrostatic compensation) relative to the actual observed depth of adult steelhead in the Bonneville Dam tailrace (top) and the Ice Harbor Dam tailrace (bottom) during the spring and summer of 2000.

Adult steelhead encountered water with total gas saturation levels at or below 115% in the Bonneville and Ice Harbor tailraces, 77% and 100% of the time, respectively (Figure 12). When the gas saturation of the water downstream from Bonneville Dam exceeded 125% TDGS, we found an increase in the percentage of time fish were exposed to a level of saturation due to inadequate depth compensation (Figure 12). At dissolved gas saturation levels between 125-130% uncompensated exposure was estimated to be 34.4% of the time (Figure 12).

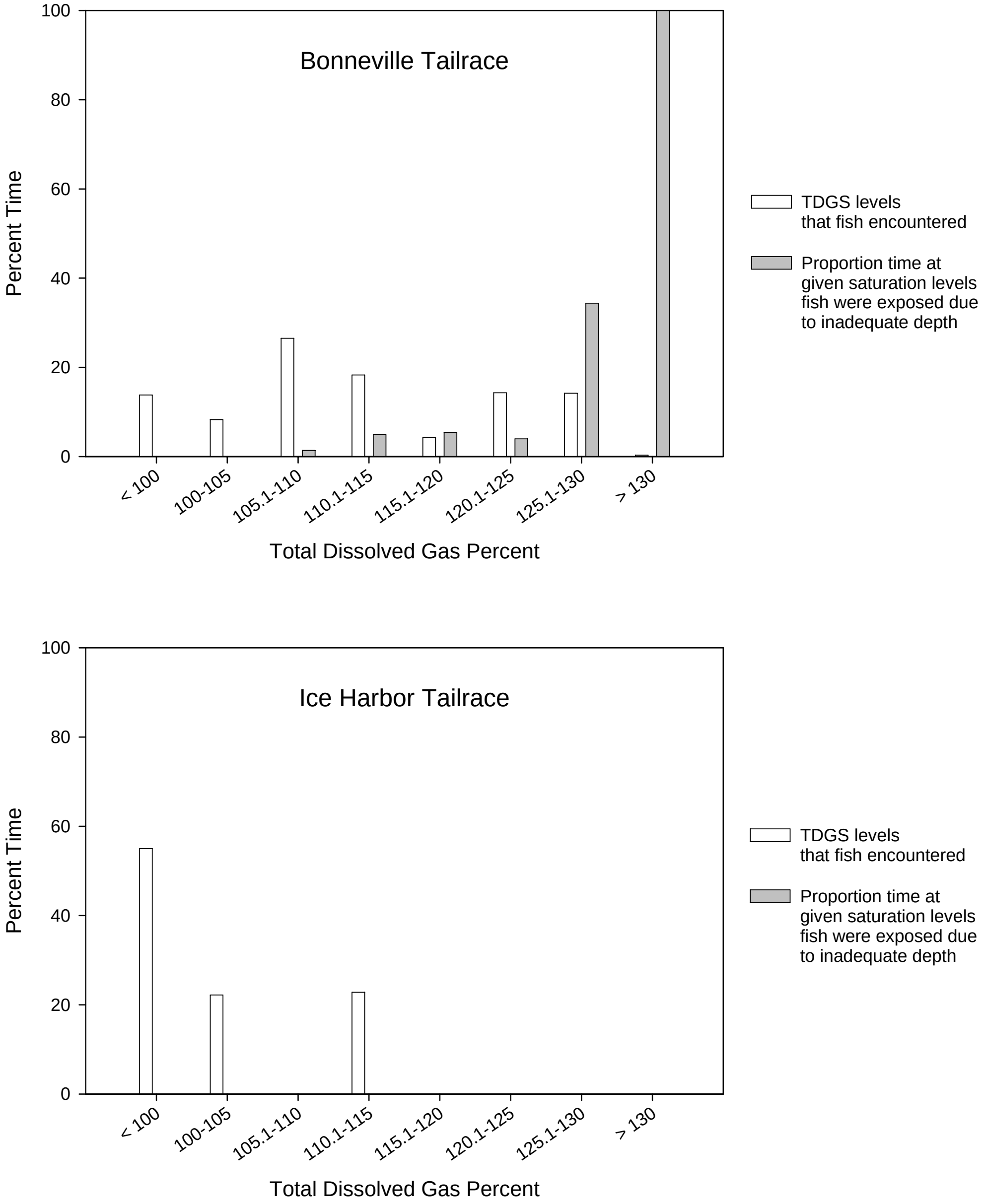


Figure 12. Total proportion of depth uncompensated exposure relative to the proportion of time at spent in water with different dissolved gas concentrations.

Large-scale Evaluation of Exposure

Of the 201 adult steelhead tagged with RDSTs, 137 tags were recovered (68% recovery rate) and 115 were used to evaluate depth of migration. Twenty-two RDSTs were unusable due to a malfunctioning pressure sensor or radio, improper tag set-up, or insufficient telemetry records. Of the 137 RDSTs recovered 38% were recaptured at the adult trap at Lower Granite Dam, 34% from the mainstem Columbia River (hatcheries, tribal and sport fishery). The remaining tags were recovered from Columbia and Snake River tributaries (Appendix Table 1). Based on last telemetry records of fish at fixed receiver sites, 36% (23 tags) were detected last upstream of Priest Rapids or Lower Granite dams, 34% (22 tags) in the lower Columbia River downstream of John Day Dam, and 30% (19 tags) between Priest Rapids or Lower Granite dams and John Day Dam.

The median depth of most individuals migrating through lower Columbia and Snake reservoirs and dam tailraces were deeper than 2-3 m. Median migration depths of adult steelhead were significantly deeper in the Bonneville Reservoir compared to Lower Monumental Reservoir (repeated measures ANOVA df = 6, 23.1, F = 5.8, P < 0.001, Figure 13). No significant differences were observed in median migration depths among lower Columbia and Snake River tailraces (repeated measures ANOVA df = 7, 53.1, F = 1.26, P = 0.30, Figures 14). Median migration depths were significantly shallower in Bonneville (Mann-Whitney Test, Z = 7.03, P < 0.001) and The Dalles (Z = -5.96, P < 0.001) reservoirs during the spill season (Figure 15). No significant relationships existed in the median depth of migration between spill seasons in John Day Reservoir (Mann-Whitney Test, Z = -0.74, P = 0.46; Figure 15). Conversely, we found that the median migration depth was significantly deeper during the spill season in the McNary Reservoir (Mann-Whitney Test, Z = 4.27, P < 0.001; Figure 15). Comparisons were not made for Ice Harbor, Little Goose, and Lower Monumental reservoirs due to insufficient depth data during the spill season. Median migration depths for adult steelhead typically increased after mid to lat July, coinciding with the reduction of spill at Columbia and Snake River dams (Figure 16).

Adult steelhead swam at depths deeper than 2 m a majority of the time when migrating through reservoirs and dam tailraces in the lower Columbia and Snake rivers. The percentage of time fish were at least 2 m below the surface (providing at least 20%

hydrostatic pressure compensation) during migration through a reservoir ranged from 64.1% at Ice Harbor to 83.2% at Bonneville (Figure 17). Fish were deeper than 1 m (providing at least 10% hydrostatic pressure compensation) ranging from 90.4% of the time in the Lower Monumental Reservoir to 97.7 % of time in the The Dalles Reservoir (Figure 16). Except for Bonneville reservoir, adult steelhead migrated deeper in dam tailraces than in reservoirs. The percentage of time spent at least 2 m below the surface during migration through a dam tailrace ranged from 51.5% at Bonneville to 94.6% at McNary (Figure 17). The percentage of time deeper than 1 m ranged from 76.6% in the Bonneville tailrace to 98.7% in McNary and Lower Monumental tailraces (Figure 17).

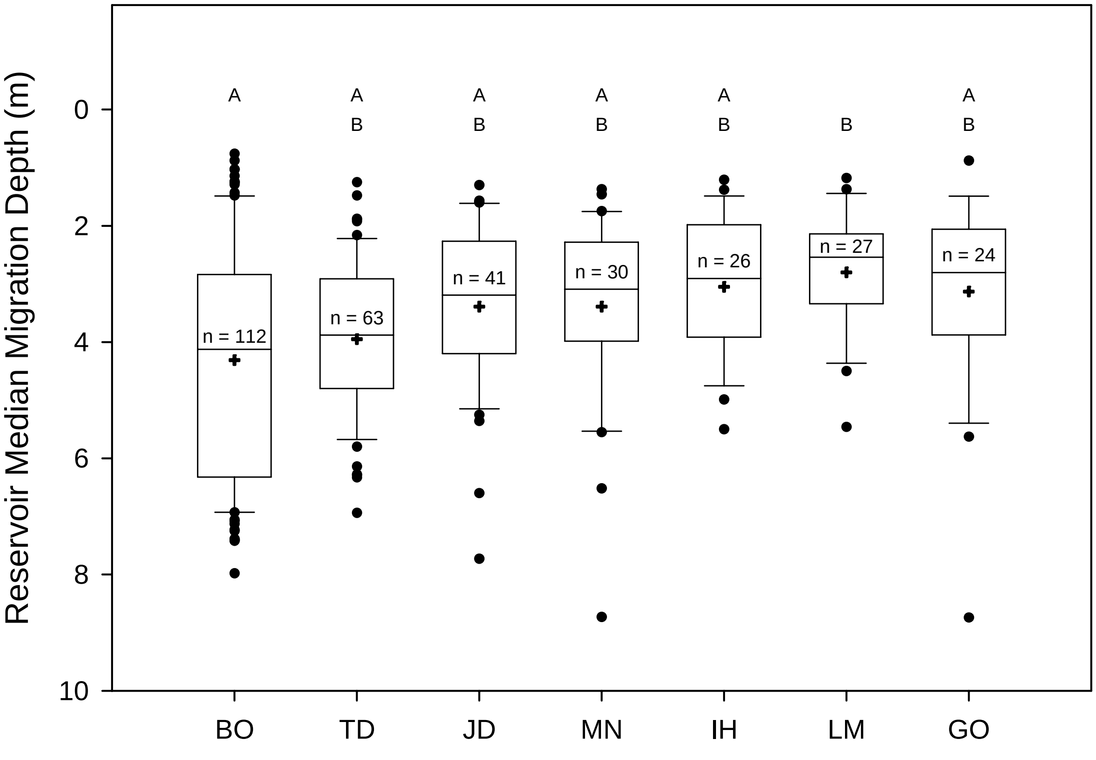


Figure 13. Mean (cross), median (bar) and 5th, 25th, 75th, and 95th percentiles of median migration depths for adult steelhead during migration through the four lower Columbia and three lower Snake River reservoirs in 2000 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, and GO = Little Goose). Median significantly different at $p = 0.05$ indicated by different letters (Tukey's *post hoc* test).

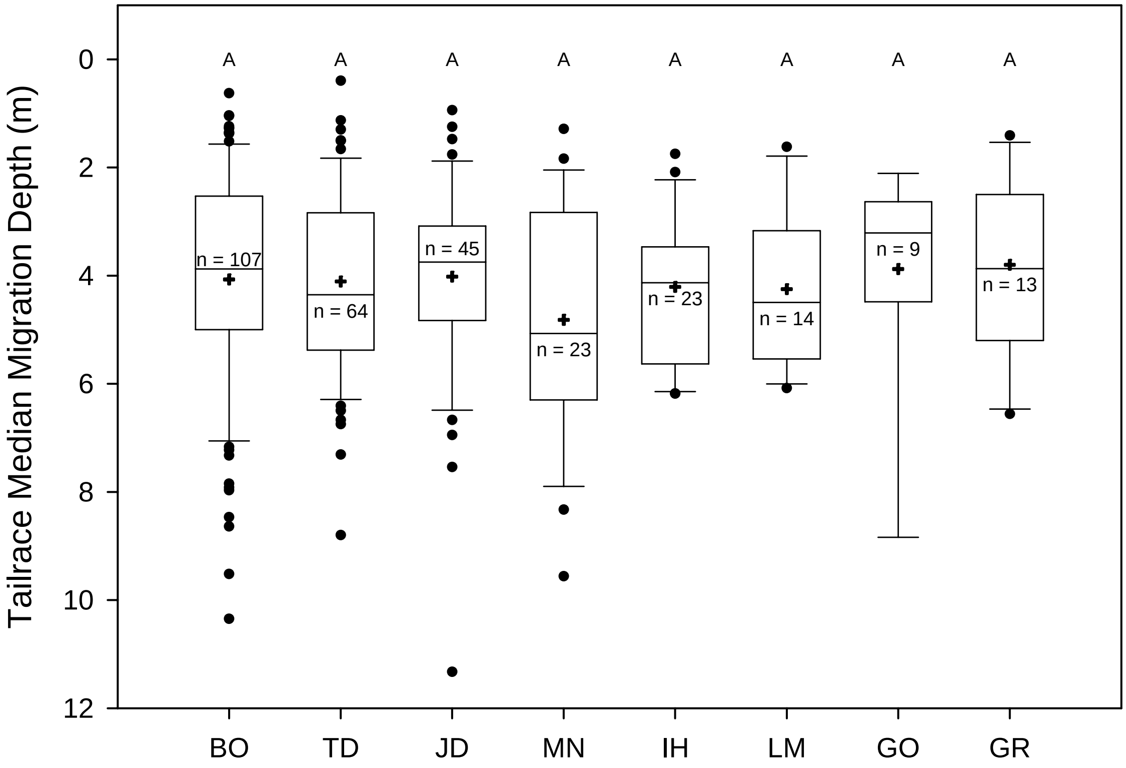


Figure 14. Mean (cross), median (bar) and 5th, 25th, 75th, and 95th percentiles of median migration depths for adult steelhead in the tailrace sections of the four lower Columbia River dams and four lower Snake River dams in 2000 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, and GR = Lower Granite). Median significantly different at $p = 0.05$ indicated by different letters (Tukey's *post hoc* test).

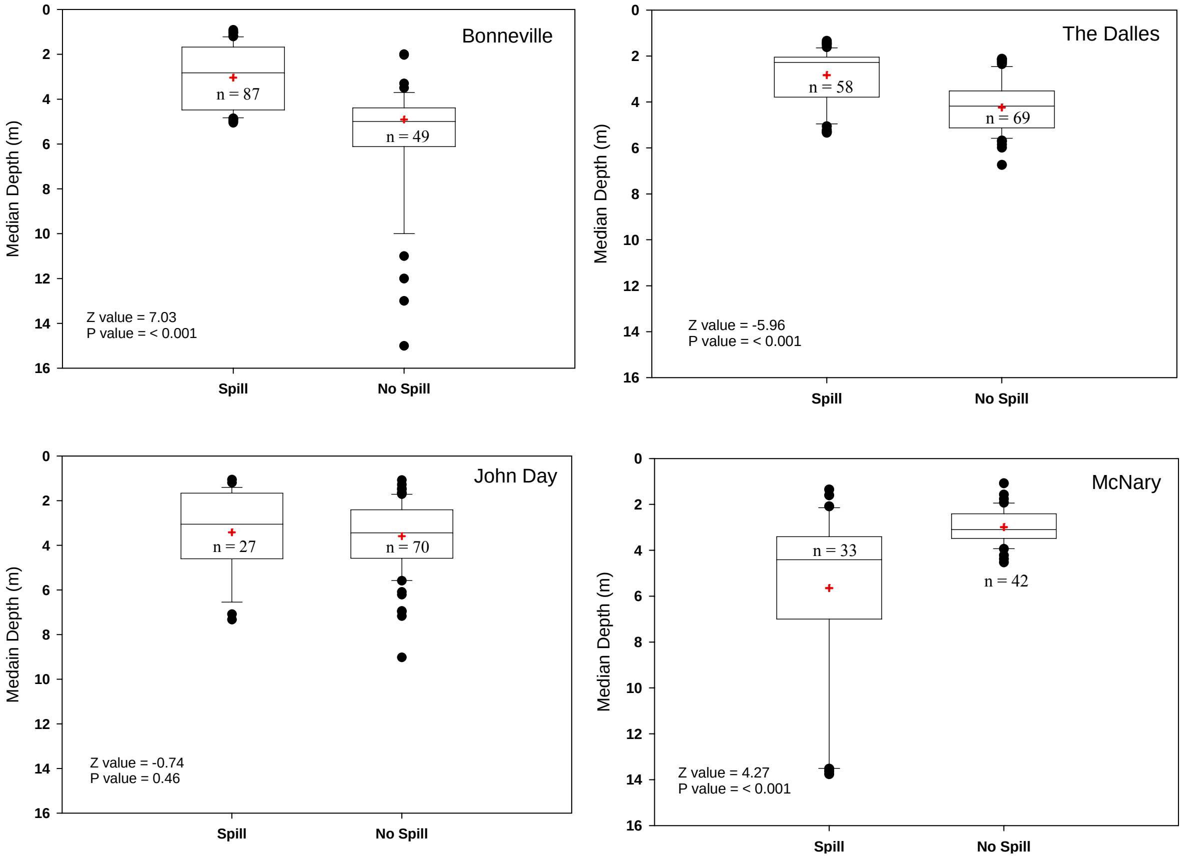


Figure 15. Mean (cross), median (bar) and 5th, 25th, 75th, and 95th percentiles of median migration depths for adult steelhead in the four lower Columbia River reservoirs in 2000 during spill and no spill conditions. Depth data is not available for adult steelhead migration at Ice Harbor, Lower Monumental, and Little Goose reservoirs during the spill season. Comparisons were made using a Mann-Whitney test.

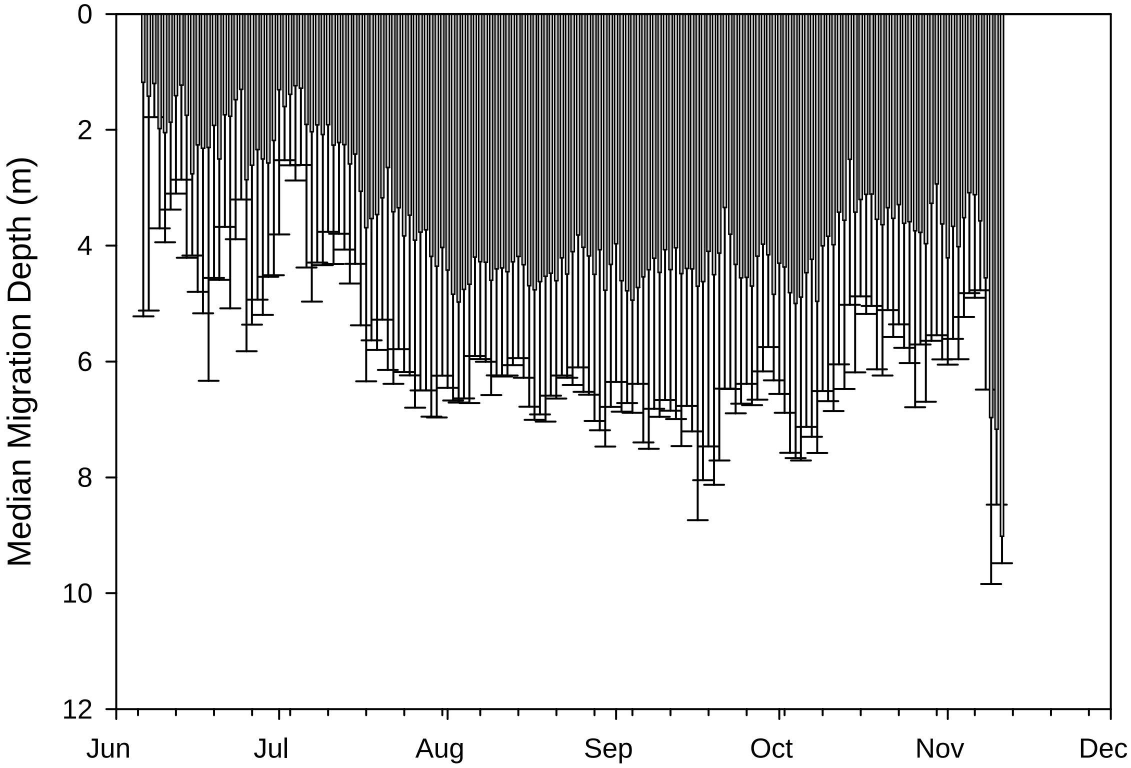


Figure 16. Median migration depths (bars) and standard deviation (whiskers) for adult steelhead migrating through lower Columbia and Snake River reservoirs during 2000.

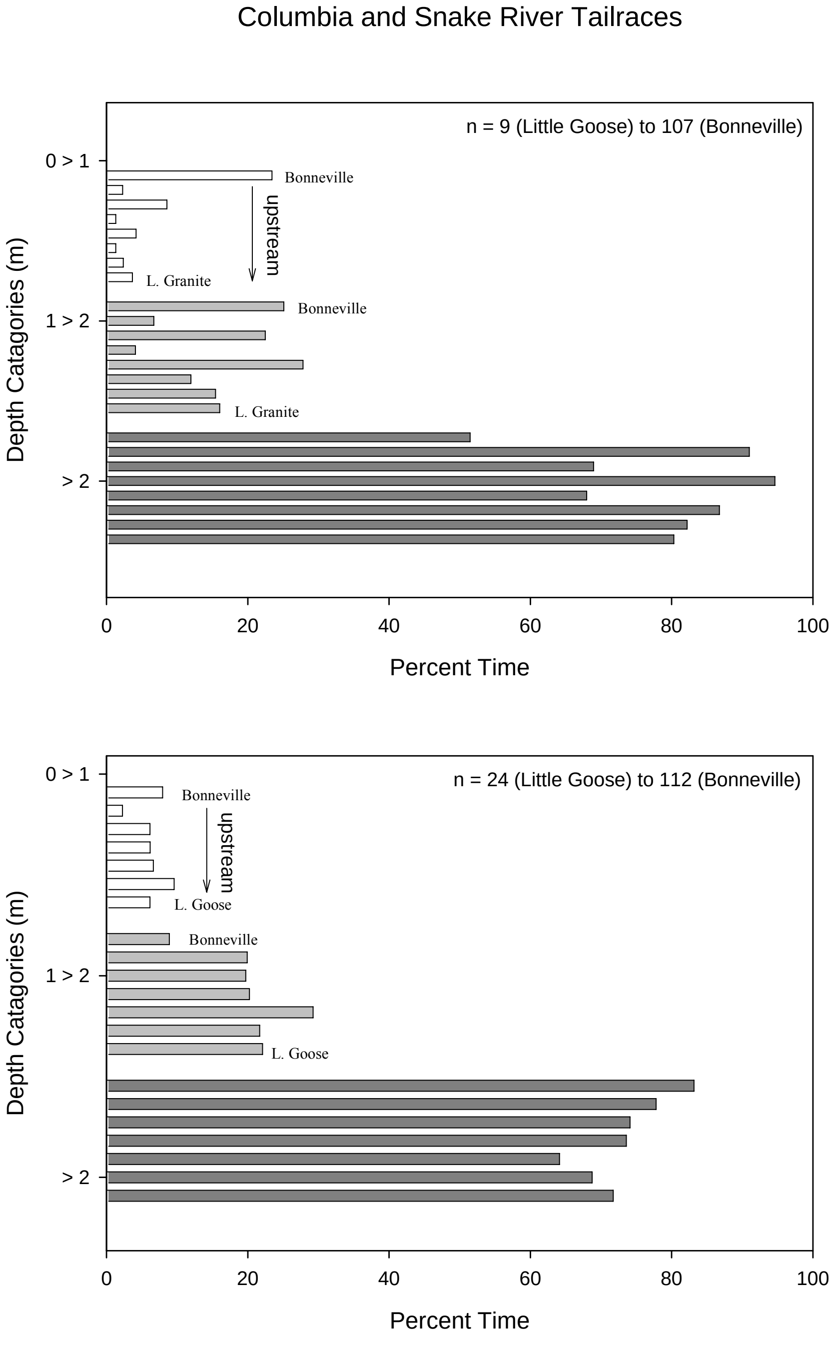
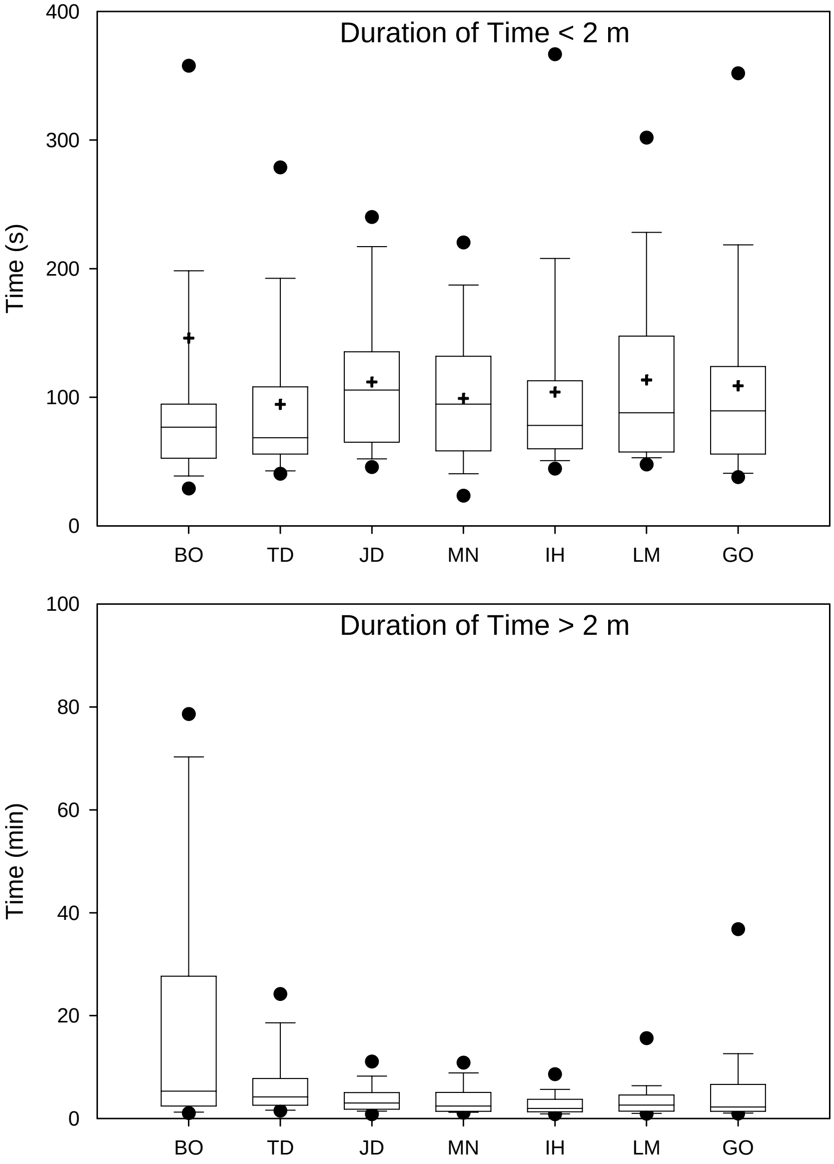


Figure 17. Percentage of time spent between the surface and > 2 m by adult steelhead tagged with radio data storage tags (RDSTs) during migration through tailraces (top panel) and reservoirs (bottom panel) in the Columbia and Snake rivers. Bars represent the percentage of time (pooled for all fish) spent at a given depth in each reservoir and dam tailrace.

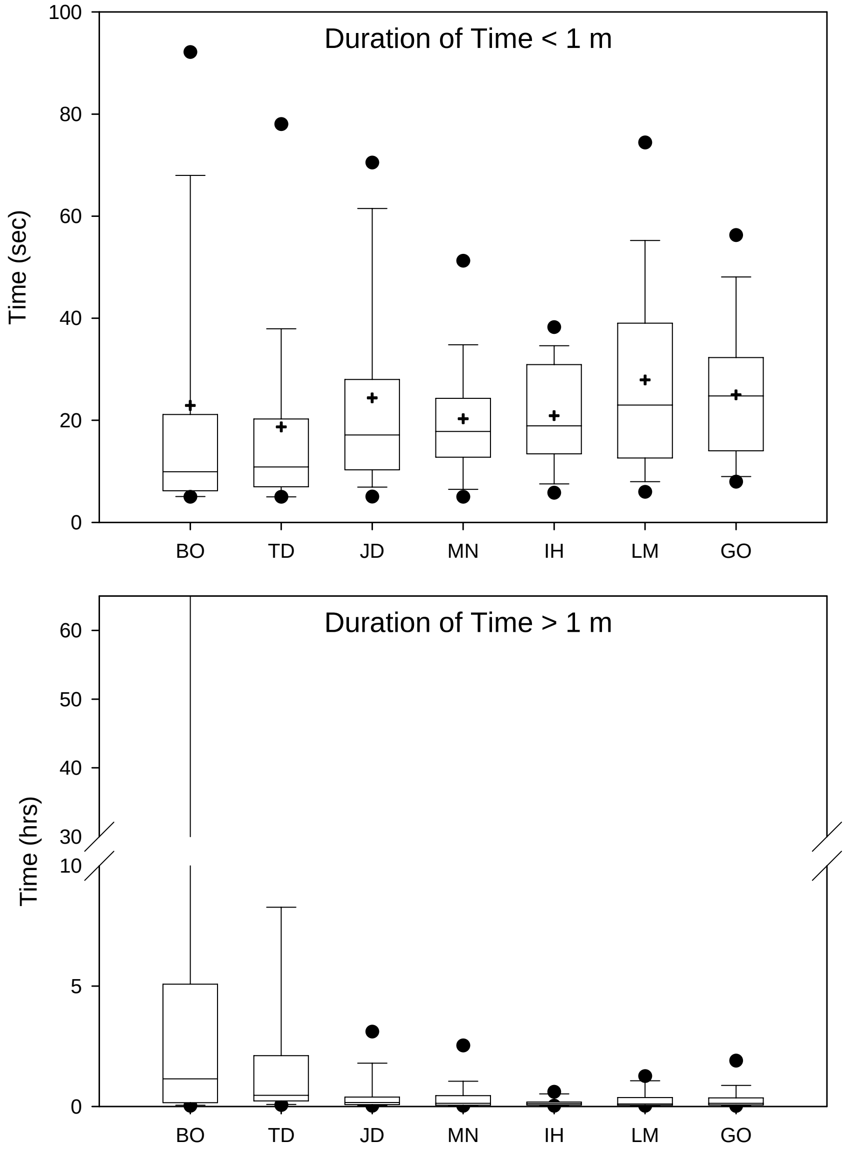
Duration of Exposure

Adult steelhead frequently altered their depth in the water column. The duration of time adult steelhead typically occupied surface waters ranged from minutes at a time at depths < 2 m to seconds at depths < 1 m (Figure 18 and 19). However, some fish were observed spending several consecutive hours at depths shallower than 1 m and several consecutive days at depths shallower than 2 m. The maximum successive time < 1 and < 2 m observed by an individual fish outfitted with a RDST was 17 h and 8.5 d, respectively (Figure 20 and 21). Although durations of time near the surface were typically short, we found that adult steelhead frequently re-ascended to surface waters. The median duration of time > 2 m deep in the water column before re-ascending to a depth < 2 m ranged from 2.0 min (Ice Harbor Reservoir) to 5.3 min (Bonneville Reservoir; Figure 18). The median duration of time > 1 m deep in the water column before re-ascending to a depth < 1 m ranged from 6 min (Lower Monumental Reservoir) to 68 min (Bonneville Reservoir; Figure 19). However, steelhead in lower reservoirs (i.e. Bonneville and The Dalles) with long durations above 2 m were in cool water plumes of tributaries based on RDST temperature records (Figure 22). And fish with short durations above 2 m based on RDST temperature records were found not to be in the influence of cool water tributary plumes (Figure 23).



*Note different scale and units (y-axis) of top and bottom plots

Figure 18. Mean (cross), median (bar), and 5th, 10th, 25th, 75th, 90th, and 95th percentiles for consecutive time (s) < 2 m (top panel) and (min) > 2 m (bottom panel) by adult steelhead during migration through lower Columbia and Snake River reservoirs. BO = Bonneville (n = 112), TD = The Dalles (n = 63), JD = John Day (n = 41), MN = McNary (n = 30), IH = Ice Harbor (n = 26), LM = Lower Monumental (n = 27), and GO = Little Goose (n = 24).



*Note different scale and units (y-axis) of top and bottom plots

Figure 19. Mean (cross), median (bar), and 5th, 10th, 25th, 75th, 90th, and 95th percentiles for consecutive time (s) < 1 m (top panel) and (hrs) > 1 m (bottom panel) by adult steelhead during migration through lower Columbia and Snake River reservoirs. BO = Bonneville (n = 112), TD = The Dalles (n = 63), JD = John Day (n = 41), MN = McNary (n = 30), IH = Ice Harbor (n = 26), LM = Lower Monumental (n = 27), and GO = Little Goose (n = 24).

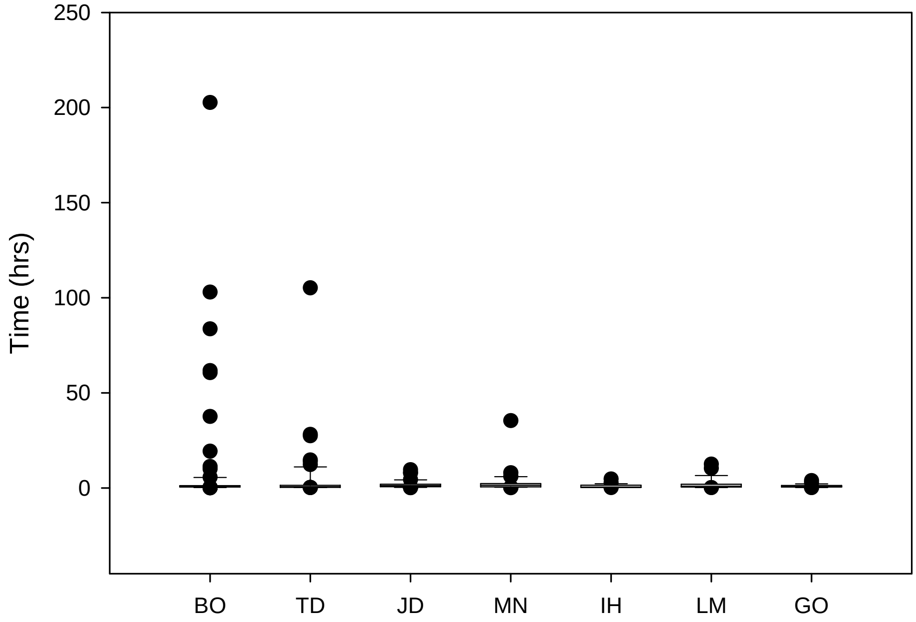


Figure 20. Maximum consecutive time (hrs) < 2 m observed by adult steelhead during migration through the four lower Columbia and three lower Snake River reservoirs. BO = Bonneville (n = 112), TD = The Dalles (n = 63), JD = John Day (n = 41), MN = McNary (n = 30), IH = Ice Harbor (n = 26), LM = Lower Monumental (n = 27), and GO = Little Goose (n = 24).

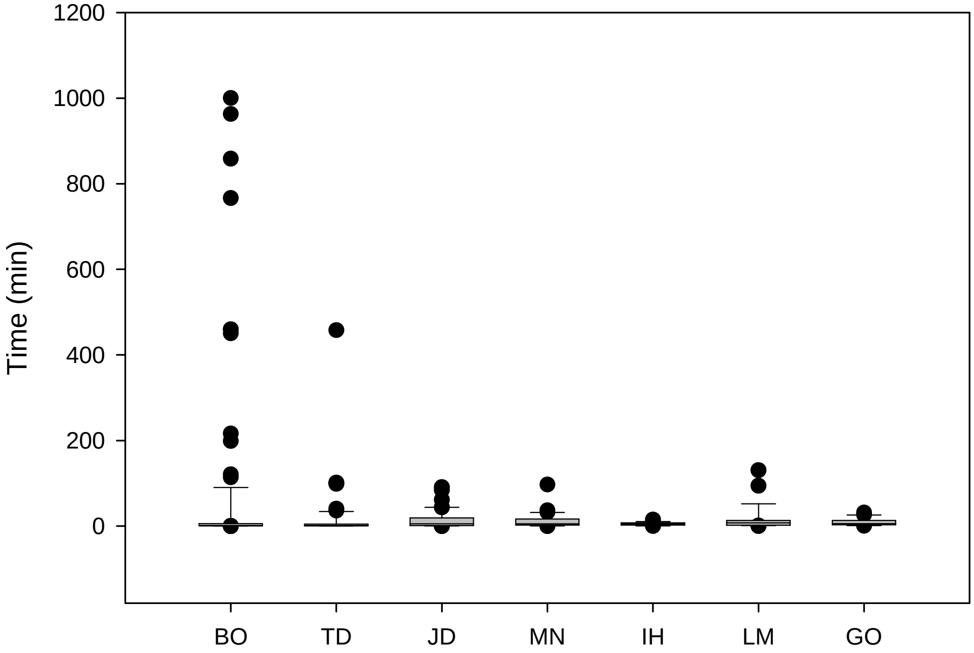


Figure 21. Maximum consecutive time (min) < 1 m observed by adult steelhead during migration through the four lower Columbia and three lower Snake River reservoirs. BO = Bonneville (n = 112), TD = The Dalles (n = 63), JD = John Day (n = 41), MN = McNary (n = 30), IH = Ice Harbor (n = 26), LM = Lower Monumental (n = 27), and GO = Little Goose (n = 24).

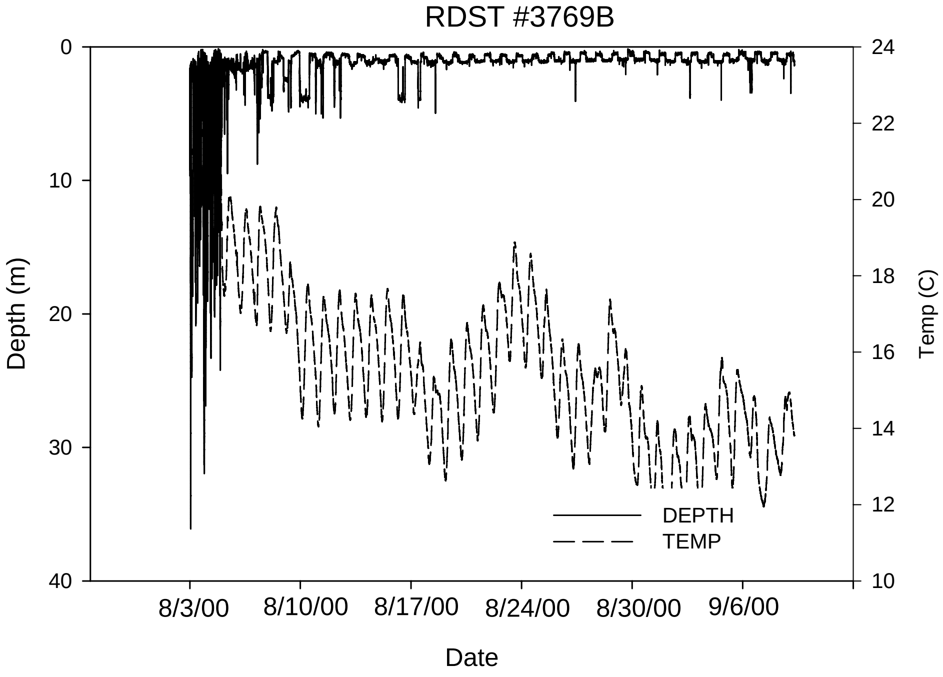


Figure 22. Swimming depth and body temperature for steelhead (RDST #3769B) from 3 August – 11 September 2000 in Bonneville Reservoir. Example illustrating that steelhead with the longest durations near the surface were in the influence of a Columbia River tributary (cooler body temperatures).

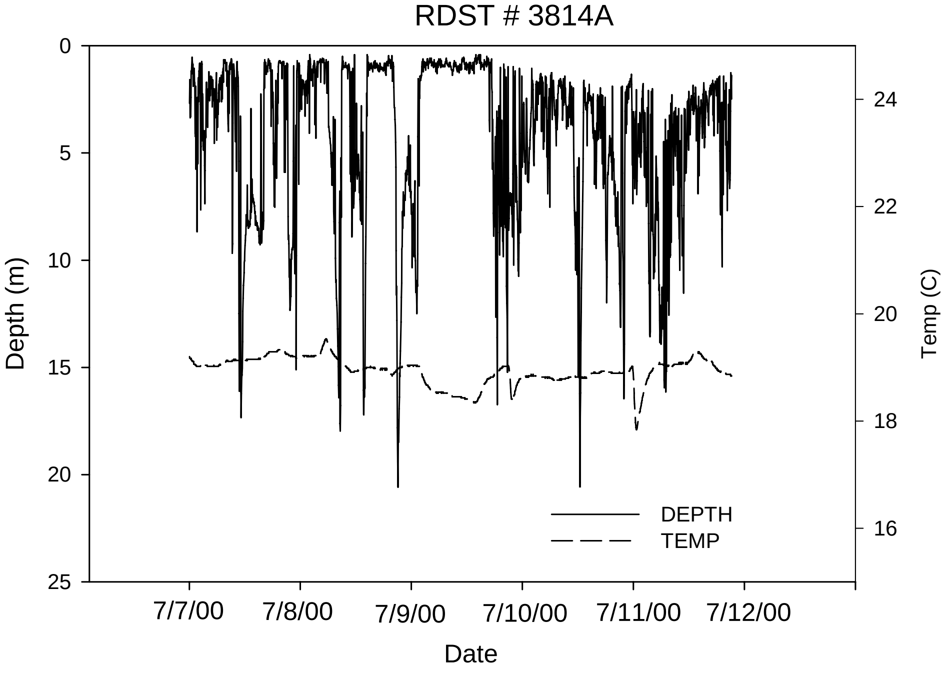


Figure 23. Swimming depth and body temperature for steelhead (RDST #3814A) from 7 July -12 July 2000 in Bonneville Reservoir. Example illustrating that steelhead with shorter durations near the surface was not in the influence of a Columbia River tributary (warmer body temperatures).

Discussion

Fine-scale Evaluation of Dissolved Gas Exposure

Results from models of dissolved gas supersaturation relative to migration depth of adult steelhead downstream from Bonneville and Ice Harbor dams indicate that depth uncompensated exposure to gas supersaturation was minimal (less than 10%) during 2000. Most of the exposure that did occur based on the modeled dissolved gas concentrations and migration depth data was equivalent to a level of saturation less than 115%. These exposure levels are lower than those generally considered lethal even with prolonged exposure (Ebel et al. 1975; Nebeker 1973).

Model results and corresponding migration depths indicated that occurrences of exposure to dissolved gas increased for adult steelhead when saturation levels exceeded 125%. Steelhead where observed most of the time migrating when saturation levels were lower than 115%, however, when saturation levels of the water exceed 125% TDGS we found an increase in the proportion of uncompensated exposure relative to the amount of time spent at these elevated levels. Dissolved gas levels higher than 125% TDGS can occur in the Columbia and Snake rivers, particularly during high-flow-high-spill years (i.e. 1996, 1997) and extended exposure at these levels can be dangerous, particularly in shallow areas of the river where the ability to hydrostatically compensate is limited.

Signs of GBD and mortality have been observed with adult Chinook salmon and steelhead in the Columbia River when saturation levels ranged between 123%-143% (Beiningen and Ebel 1970). Ebel et al. (1975) found that even when adult salmon were allowed to hydrostatically compensate, substantial mortality occurs when gas saturation levels exceed 120% for more than 20 d due to insufficient depth compensation. In particular, there may be locations with potential for high exposure such as the areas north of Pierce and Ives Islands, where many fish were observed, depths are relatively shallow, but gas levels were not modeled. Occurrences of extreme dissolved gas levels are likely lower than in the past because of modifications (addition of flow deflectors at spillways) and operational changes.

Our estimates of dissolved gas exposure histories for adult migrants were probably conservative because of the tendency for the dissolved gas model to overestimate saturation levels (Richmond et al. 1999). Model verification results indicated that the

MASS2 model simulations accurately modeled the spatial variability in dissolved gas concentrations, but the estimated total dissolved gas concentrations were consistently higher (2-5%) than those observed in the field, with some estimates being as much as 20% higher than actual (Richmond et al. 1999). Inaccuracies of the RDSTs, may have accounted for an additional 5% error in estimating the degree of uncompensated exposure.

Adult steelhead did not move laterally to avoid higher dissolved gas concentrations (>120% TDGS). Approximately equal proportions of fish entered higher dissolved gas water as compared to fish that left areas of the river with elevated dissolved gas levels. These results conflict with lab tests in shallow tanks where juvenile Chinook salmon actively avoided 120% and 130% nitrogen supersaturated water (Meekin and Turner 1974; Dawley et al. 1975; Stevens et al. 1980). Since we monitored migration paths of adult fish migrating in-river, we were unable to account for effects of hydrostatic compensation making our results difficult to compare to laboratory studies. The short periods spent near the surface followed by return dives to deeper (> 2m) water could be interpreted as individual fish responding to the physiological effects of supersaturated tissues as they entered pressure conditions near the surface conducive to gas bubble formation. However, steelhead tagged when average TDGS were < 105% exhibited qualitatively identical patterns of frequent and rapid depth changes. Alternatively, adult steelhead may not have been aware of existing gradients in TDGS at the scale of the whole river, perhaps because of efforts to move across river channels to sample gas concentrations may represent a greater energetic cost than risk from exposure or migration at deeper depths. Similarly, steelhead may not have the sensory capabilities to recognize supersaturated water since high saturation levels and selection for avoidance behavior has been historically absent. Explanations for the apparent lack of vertical avoidance could reflect a searching behavior. In open water salmon may frequently move between different layers within the water column to gain information about the chemical composition to facilitate orientation to home stream odors (Doving et al. 1985; Doving and Stabell 2003). This mechanism would require a fish to continuously change its position in the water column particularly if the interface of adjacent layers becomes indistinct (Doving et al. 1985) and would minimize the amount of time spent in surface waters. Such behavior may explain the continuous up and down movements in the water column that we observed.

Adult steelhead oriented near shorelines during upstream migration regardless of the position of the dissolved gas plume. Migration in close proximity to shorelines has been previously documented for adult Chinook salmon (Bjornn et al. 2000; Reischel and Bjornn 2003; Hughes 2004) and steelhead (Monan et al. 1970). A possible explanation is that orientation to shorelines may be an energy-conserving behavior as fish seek slower water velocities near shore. Migrating close to shore may also put fish in better position to detect chemical cues from the natal tributaries, thus reducing the likelihood of straying. Steelhead were observed mid-river only when crossing between shorelines. We found that crossing was more frequent where a tributary flowed into the river from the opposite shoreline, or where a shallow shelf extending into the river directed fish to the opposite shoreline.

In summary, we observed that adult steelhead migrated near shorelines during upstream migration. Operational changes at the dam that could direct the dissolved gas plume mid-river would reduce the risk of encountering water with higher dissolved gas conditions. Dissolved gas levels were moderate in 2000 and degree of exposure (post depth compensation) to supersaturated water was minimal. Exposure that did occur as a result of inadequate depth compensation was generally less than reported levels known to cause signs of severe GBD and mortality for adult salmonids. We did not observe strong associations between migration routes and the dissolved gas concentration of the water, which, may be the result of a fish's inability to avoid supersaturated water or possibly the lack of biological effects to TDGS as a result of the fish's depth.

Large-scale Evaluation of Dissolved Gas Exposure

We found that adult steelhead migrating through reservoirs and tailraces in the lower Columbia and Snake rivers spent a majority of their time at depths that provided adequate hydrostatic compensation for supersaturated conditions in the range of 120% or more. The observed depth-use of adult steelhead may explain the relatively low incidence of GBD in adult steelhead sampled at Bonneville Dam when gas supersaturation levels are lower than 120-125% (Backman and Evans 2002). Migratory depths of steelhead were similar to adult Chinook salmon under similar dissolved gas conditions (Gray and Haynes 1977; Johnson et al. 2004).

The combination of the extent of TDGS and the frequency and duration of descents deeper than compensation depth largely determines the development and severity of GBD (Weitkamp and Katz 1980; Elston et al. 1997; Hans et al. 1999; Weitkamp et al. 2003). Results of past studies indicate that GBD symptoms become more detrimental as duration of exposure increases (Weitkamp and Katz 1980). Based on reservoir passage times of up to several days, adult steelhead could potentially be exposed to gas supersaturation for long periods (Keefer et al. 2004a). However, although steelhead frequently entered the upper 2 m of the water column, excursions to shallow depths were typically brief, ranging from seconds for depths less than 1 m to minutes for depths less than 2 m. Effects of short but frequent exposure patterns that we observed in adult steelhead on the prevalence of GBD and mortality are not well understood. Previous studies have shown that intermittent deep and shallow water exposure produced less signs of GBD and mortality than fish that are unable to change depths (Dawley et al. 1975; Ebel et al. 1975; Weitkamp 1976; and Knittel et al. 1980).

Due to the number of variables involved, the time required for the formation of emboli that would result in the physical appearance of GBD and mortality can vary considerably. The appearance of bubbles involved both their formation and growth to a size that blocks vascular flow. These times can vary as a result of interindividual susceptibility to GBD, location of emboli formation, fish depth, duration of compensatory depths in addition to other modifying influences e.g., presence of residual bubbles, activity of the fish, and water temperature (Weitkamp and Katz 1980; Hans et al. 1999; Mesa et al. 2000; Morris et al. 2003). Available literature suggests significant bubble formation requires periods of tens of minutes to hours of uncompensated exposure, and fish with supersaturated tissues would unlikely experience signs of GBD given the time scale of shallow-water use we observed. Morris et al. (2003) observed bubbles in the lateral of juvenile Chinook salmon after the first hour of exposure at 125% and 130% TDGS. Mesa et al. (2000) observed complete occlusion of the lateral line after 2 h exposure at 130% TDGS and 50% occlusion after 14 d exposure at 110% TDGS. Continuous vertical movements were observed in juvenile steelhead in a deep (10 m) aquarium and no mortality was observed within 7 d at total dissolved gas levels of 130% (Dawley et al. 1975).

The longest durations of time spent near the surface (< 2 m) occurred in the Bonneville Reservoir, a reach with many tributaries. We observed some steelhead spending several consecutive days at depths shallower than 2 m. However, based on temperature data from RDSTs, these fish had cooler body temperature suggesting they were in the influence of a Columbia River tributary where gas saturation levels would be near normally saturated (i.e. 100-105% TDGS). Even the longest continuous time recorded by an adult steelhead at depths < 1 m (17 h) would probably be insufficient to affect reproductive success or cause severe GBD symptoms or mortality based on in-river dissolved gas levels in 2000. Continuous exposure to gas supersaturated water, 45 h at 114% TDGS and 10 hr 125% TDGS in 0.5 m deep tanks had no effect on pre-spawn mortality or reproductive success of female Chinook salmon late in their maturation (Gale et al. 2004). Ebel et al. (1975) reported that 25 d continuous exposure was needed to cause substantial mortality in both juvenile and adult salmon confined to shallow water (1 m) at a saturation level of 115% TDGS. Nebeker (1973) indicated that the lethal time that results in death of one-half of the exposed population (LT50) for adult Chinook salmon at 125% TDGS in a shallow tank was approximately 17 h.

Frequent dives into the water column (below the hydrostatic compensation depth) may provide an opportunity to recover from exposure to supersaturation as a result of gas bubble reabsorption. For fish remaining below the compensation depth, gas in the form of bubbles will eventually be transferred into plasma or cellular fluids (Elston et al. 1997). The time it takes for bubble reabsorption can vary depending of GBD severity, location of bubbles, and the pressure differential (Elston et al. 1997; Hans et al. 1999). Rapid bubble reabosption (5 min) was observed in yearling Chinook salmon exposed to hydrostatic pressure equivalent to 30 m (Elston et al. 1997). Rapid recovery from potentially lethal effect of supersaturation can also occur when moving from water with high supersaturation to water with near normal supersaturation (Hans et al. 1999). Lateral gradients of supersaturated water that exist downstream of dams and tributaries in the lower Columbia River may provide refuge from gas supersaturated water (Scheibe and Richmond 2002). Although our results do not prove that bubble reabsorption is actually occurring in upriver migrants, the observed depth histories indicate that bubble reabsorption is possible.

Many lower Columbia and Snake River dams increased spill volume during the nighttime to take advantage of the tendency of juvenile salmonids to pass dams at night (Brege et al. 1996). However, these increases in spill generally resulted in small increases in TDGS levels (< 5%) recorded by monitoring stations (U.S. Army Corps of Engineers 1998). Results were inconclusive regarding adult steelhead migration during periods of spill and no spill. Median migration depths for adult steelhead typically increased after mid to late July, coinciding with the reduction of spill at Columbia and Snake River dams. Migrating deeper in the late summer and early fall also could be a response to increased water temperatures.

Unaccounted for RDSTs could have potentially biased our results because fish experiencing uncompensated exposure as a result of shallow migration would be less likely to successfully reach lower Granite Dam or other destinations where the transmitter could be found and returned. However, based on last telemetry records at dams, 36% of the unaccounted for fish were detected either upstream of Priest Rapids Dam (rkm 638.9) in the Columbia River or Lower Granite Dam (rkm 694.6) in the Snake River. Radio transmitter return rates are substantially lower for the upper Columbia and Snake rivers as a result of reduced coverage and tag recovery effort. Telemetry records indicate that 34% of the unaccounted for fish were last detected in the lower Columbia downstream of John Day Dam where transmitter regurgitation rates were highest (Keefer et al. 2004b). Given the general lack of evidence for the effects of GBD the fact that most unaccounted for fish migrated out of the lower Columbia and Snake rivers suggests that this source of error did not seriously bias our results.

In conclusion, evaluation of adult steelhead migration depths indicates that the majority of time was spent at depths that provided adequate compensation for supersaturated conditions in the range of 120% of saturation or more. We did not observe strong associations between migration depth near the surface and the dissolved gas concentration of the water. The weak associations we found may be the result of a fish's inability to detect and avoid water conditions favoring bubble formation or the lack of highly supersaturated conditions (i.e. > 120% TGDS) conditions in-river. We caution that greater TDGS and behavioral responses may occur in years with higher discharge and spill conditions. Fish entered surface waters (< 2m) frequently, but the time spent there was usually brief. Steelhead spending extensive durations near the surface (days < 2 m) were likely near the mouth of a tributary where TDGS would be reduced based on body temperatures cooler than the mainstem Columbia River. The apparent vertical movement into and out of the surface layers by adult steelhead suggests the need for additional research to identify effects of frequent but short durations of depth uncompensated exposure on long-term survival and reproductive fitness.

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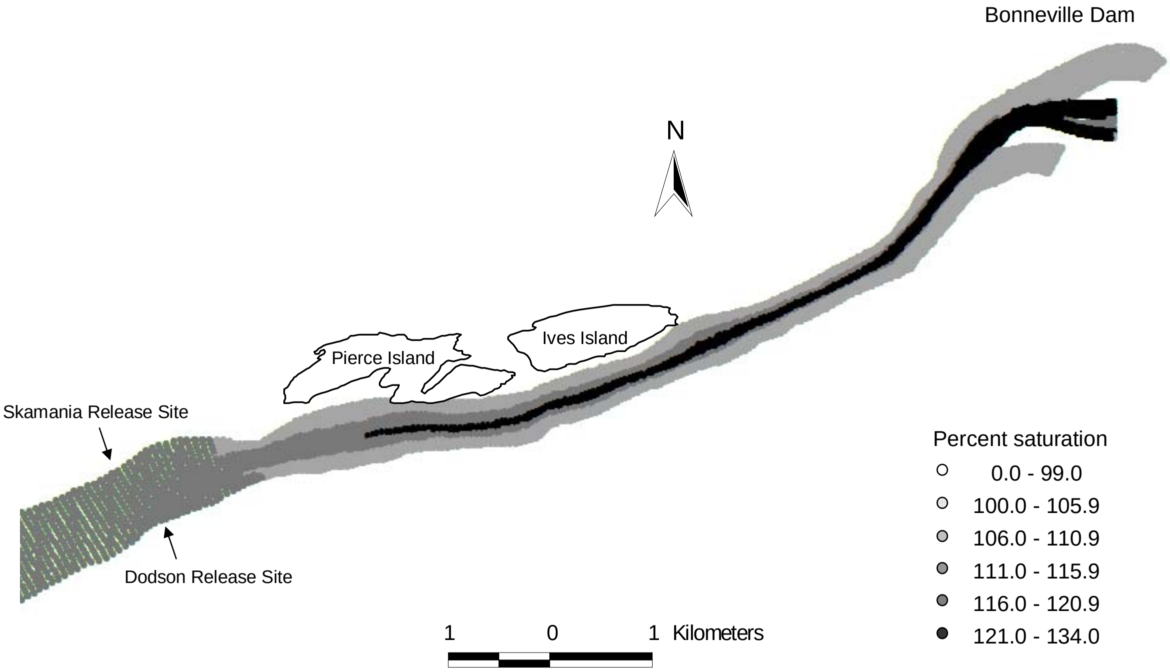
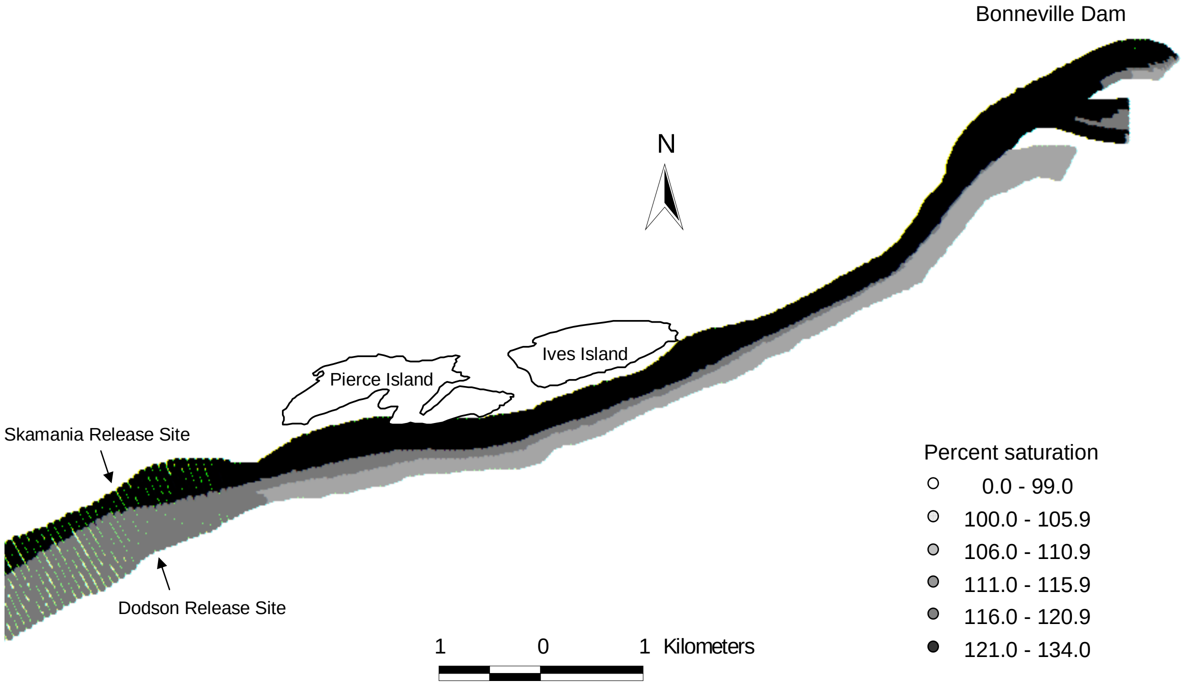
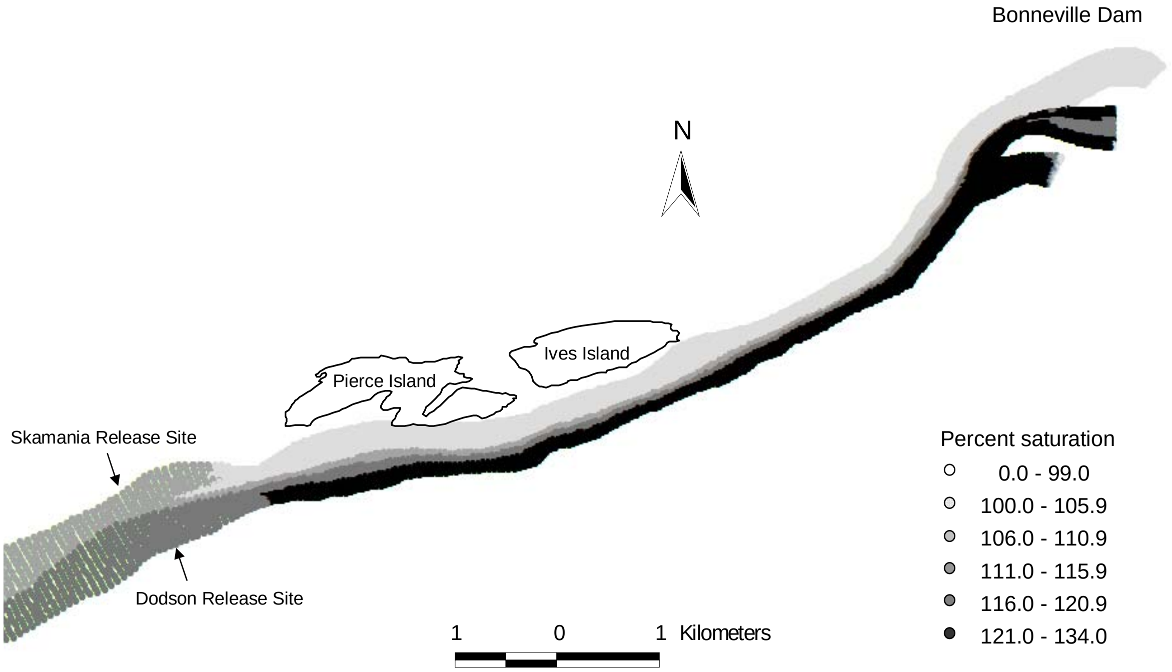
Appendix



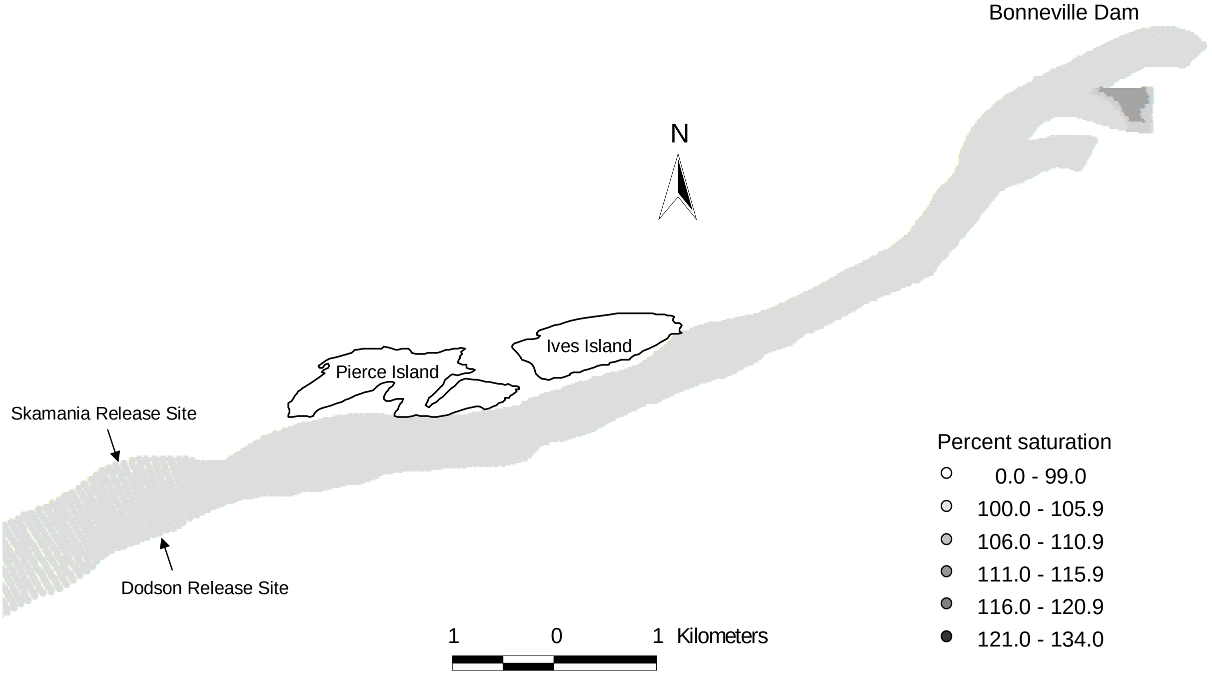
Appendix Figure 1. MASS2 simulated dissolved gas saturation downstream of Bonneville Dam on 29 April 00 during spill (119,000 cfs), discharge from powerhouse 1 (100,000 cfs) and discharge from powerhouse 2 (88,887 cfs).



Appendix Figure 2. MASS2 simulated dissolved gas saturation downstream of Bonneville Dam on 4 June 00 during spill (102,000 cfs), discharge from powerhouse 1 (97,350 cfs) and discharge from powerhouse 2 (6,758 cfs).



Appendix Figure 3. MASS2 simulated dissolved gas saturation downstream of Bonneville Dam on 24 July 00 during spill (91,900 cfs) and discharge from powerhouse 2 (81,941 cfs).



Appendix Figure 4. MASS2 simulated dissolved gas saturation downstream of Bonneville Dam on 12 April 00 during no spill conditions, powerhouse 1 discharge (100,000 cfs) and powerhouse 2 discharge (129,854 cfs).

Appendix Table 1. Recapture location for steelhead tagged with RDSTs in 2000.

Recapture Location	***Number***	***RKM***
Lower Granite Dam Adult Trap	52	694.6
Mainstem Columbia River	47	
Klickitat River	4	290.3
Little White Salmon River	4	260.7
North Fork Clearwater River	4	810.9
Deschutes River	4	328.4
Hood River (Powerdale Dam Trap)	2	279.8
Salmon River	2	824.5
White Salmon River	2	270.8
Chiwawa River	1	831.5
Clearwater River	1	745.8
Grande Ronde River	1	793.1
Herman Creek (lower Columbia River)	1	242.5
Hells Canyon Dam (Snake River)	1	919.1
John Day River	1	350.8
Mainstem Snake River	1	521.6
Oxbow Dam (Snake River)	1	960.9
Sandy River	1	193.9
Santiam River	1	338.7
Wallowa River	1	924.0
Wenatchee River	1	753.7
Walla Walla River	1	506.0
Unknown	3	