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MIGRATION DEPTHS OF ADULT CHINOOK SALMON AND STEELHEAD IN THE LOWER COLUMBIA AND SNAKE RIVERS IN RELATION TO DISSOLVED GAS EXPOSURE, 2002

Report for project ADS-00-5

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Preface

The tagging of adult Chinook salmon and steelhead with archival depth and temperature sensitive radio transmitters (RDSTs) in 2002 was a continuation of a study started in 2000, however, fine-scale evaluation of dissolved gas exposure including dissolved gas model (MASS2) results and tracking individual fish migration routes were not performed in 2002. In this report we provide information on the in-situ depths of migration for adult Chinook salmon and steelhead migrating through the Columbia-Snake River hydrosystem in relation to the degree of hydrostatic compensation achieved to gas supersaturated water during the 2002 migration season. Fish were tagged with RDSTs because of concerns by state, federal, and tribal agencies regarding the applicability of using results from the laboratory or in-river cage experiments to evaluate in-river conditions experienced by adult Chinook salmon and steelhead because little is known about their migration depths. These concerns were reflected in the Biological Opinion in 2000 for operation of the Federal Columbia River Power System. Study objectives for this project relate specifically to RPA's 24, 107, and 115 in Section 9.6.1 of the Biological Option (NMFS 2000).

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Abstract

High spill volume at dams can create supersaturated dissolved gas conditions that may have negative effects on fishes. During 2002, 184 adult Chinook salmon Oncorhynchus tshawytscha and 231 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 dams and reservoirs of the lower Columbia and Snake rivers. These data were used to estimate the degree of exposure to gas supersaturated conditions. Migration depth plays a role in the development of gas bubble disease because hydrostatic compensation reduces the effects of exposure to supersaturation at greater depths. We found that adult spring and summer Chinook salmon and steelhead spent a majority of their time at depths deeper than 2 m (providing at least 20% hydrostatic compensation). However, migration depths below 2 m were interspersed with periods lasting several minutes at depths shallower than 2 m. Statistical associations were weak between dissolved gas concentrations and the percent and duration of time fish occupied near-surface waters. Based on the observed migration depths and dissolved gas conditions in the river, biological effects resulting from depth uncompensated exposure to dissolved gas were likely minimal in 2002.

Introduction

Impacts of mainstem dams in the Columbia River basin on anadromous salmonids, especially those from threatened and endangered stocks, have received much attention over the past 25 years (National Research Council 1996; Ruckelshaus et al. 2002). One of the central issues regarding effects of dams on fish populations is the impacts of elevated dissolved gas levels of water. Since the early 1990's, voluntarily spilling water over dam spillways has been one management strategy used to improve survival of juvenile salmonids Oncorhynchus spp. passing Columbia and Snake River dams by reducing the number of smolts passing through turbines and bypass systems (Schoeneman et al. 1961; Muir et al. 2001). Spilling at lower Columbia and Snake River projects typically begins the first week of April and continues through the end of August during which time spill volume is increased during nighttime to take advantage of the tendency of juvenile salmonids to pass dams at night (Brege et al. 1996). However, spillway discharge at dams during the spring and early summer causes atmospheric air to be entrained in the stilling basin to depths where pressure is sufficient to produce supersaturated conditions that exceed the water quality standard of 110%. Voluntary spill has raised concern about the resultant increase in dissolved gas levels on adult spring-summer Chinook salmon O. tshawytscha and steelhead O. mykiss because the spill period coincides with their upstream migration.

Gas bubble disease (GBD), also known as gas bubble trauma (GBT), is a condition that can affect fish and aquatic invertebrates residing in water that has become supersaturated with atmospheric gases. Gas bubble disease is caused by the formation of excessive bubbles in tissues and body fluids which then cause potentially lethal vascular and cardiac blockage or hemorrhaging. Bubbles form when tissues and fluids of fish become supersaturated after exposure to supersaturated water conditions and the pressures of dissolved gases in fish tissues exceed 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, fish depth plays a central role in the expression of GBD because the hydrostatic pressure has a strong influence on the total dissolved gas supersaturation (TDGS) exposure to individual fish. The hydrostatic pressure achieved by swimming

deeper in the water column inhibits formation of interstitial gas bubbles. Each meter of depth exerts pressure that increases the solubility of dissolved gas to compensate for approximately 10% of saturation (Weitkamp and Katz 1980), where 100% represents fully saturated water. A fish maintaining a constant depth of 2 meters in water saturated at 120% would experience complete compensation, whereas, a fish maintaining a depth of 1 meter would experience partial compensation (Figure 1). In addition to direct effects, GBD has also been known to increase a fish's susceptibility to disease and predation, and reduced 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; Knittel et al. 1980).

Most historical studies that have addressed exposure to dissolved gases on survival and reproductive potential have been conducted in controlled settings (laboratories and in-river cage experiments) with restrained fish (Westgard 1964; Knittel et al. 1980; Heggberget 1984; Krise and Meade 1988; Mesa et al. 2000). Furthermore, most of the focus has been with juvenile salmonids (Weitkamp and Katz 1980). An important issue is the applicability of using results from confined chambers to evaluate conditions experienced by free-swimming salmonids, since depth distributions influence the biological effects of TDGS. Objectives for this study were 1) to evaluate the migration depths of adult Chinook salmon and steelhead in a riverine environment where gas supersaturated conditions exist and 2) to evaluate associations between the migration depth of adult fish and the total dissolved gas concentration of the water as a test of whether fish altered their behavior when encountering supersaturated conditions.



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).

Methods

Study Area

The study area included the lower Columbia River from release sites at Dodson, OR and Skamania, WA (located approximately 10 km below Bonneville Dam) at river kilometer (rkm) 225.9 (measuring from the Columbia River mouth) 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).



Longitude

Figure 2. The Columbia and Snake rivers, where the migration of radio-tagged adult Chinook salmon and steelhead were monitored during 2002. All major Columbia River tributaries upstream from Bonneville Dam were monitored with radio-telemetry: 1) Wind, 2) Little White Salmon, 3) White Salmon, 4) Hood, 5) Klickitat, 6) Deschutes 7) John Day, 8) Umatilla, 9) Walla Walla, 10) Snake, and 11) Yakima.

Tagging and Monitoring Procedures

Adult Chinook salmon and steelhead were trapped and tagged at the adult fish facility located adjacent to the Washington shore fishway at Bonneville Dam. A total of 184 adult spring-summer Chinook salmon and 231 steelhead were tagged intragastrically with a 3-volt (9×2 cm; 34 g in air) radio data storage transmitter (RDST). Radio data storage transmitters were programmed to record temperature at 1-min intervals and pressure at 5-s intervals during upstream migration, which allowed approximately 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 spring-summer Chinook salmon and steelhead thought to be of Snake River origin based on either passive integrated transponder (PIT) tag codes or adipose fin clips, so that tags could be recovered at the Lower Granite Dam fish trap (Figure 2). More details on tagging methods and the adult fish facility can be found in Keefer et al. (2004a).

Chinook salmon and steelhead movements past dams, through reservoirs, and into tributaries were monitored 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. The migration history of individual fish was separated into passage segments in reservoirs and in the tailrace of dams as reported in Johnson et al. 2004. 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 and antennas (Figure 2). In addition, Eagle Creek and Herman Creek were monitored on a weekly basis from boat or truck.

Statistical Analysis

We examined patterns of depth use throughout the migration by calculating the median migration depth of each fish in each Columbia and Snake River reservoir or tailrace using the RDST data. Medians are reported and used in statistical analyses 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); using a compound symmetry covariance structure for Chinook salmon and a heterogeneous autoregressive covariance structure for steelhead. 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 tailrace were performed using a Tukey-type post hoc statistic (Zar 1999). For steelhead whose migration timing extended into the non-spill season,

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 TDGS was estimated as the percentage of time fish were observed near the surface (between 0 and 2 m) and the 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 the levels of dissolved gas encountered by the fish. 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 tissue bubble formation despite exposure to supersaturated conditions given the degree of supersaturation observed in-river (Figure 3).

Linear regression analysis was used to evaluate relationships between the gas saturation of the water and the migration depth during passage through reservoirs. The independent variable used in this regression model was the average TDG percentage weighted by the duration of time an individual fish was observed in a reservoir. Total dissolved gas concentrations were measured hourly at a depth of 2-3 m by a fixed monitoring station located in the forebay of the reservoir and tailrace of each dam on the Columbia and Snake rivers. The median migration depth, percentage of time observed deeper than 1 and 2 m, and the continuous amount of time shallower than 1 and 2 m, for individual Chinook salmon and steelhead at each dam were dependent variables in the linear regression models. Percent time spent deeper than 1 and 2 m was arcsine transformed to improve homogeneity of the variances and normality of the residuals (Zar 1999).



Figure 3. Total dissolved gas concentrations (%) measured in lower Columbia and Snake River forebays in 2000 (dotted line), 2002 (solid line), relative to the 10-year average (broken line).

Results

Chinook salmon

Of the 184 adult spring-and summer Chinook salmon tagged with RDSTs in 2000, 128 tags were recovered (70% recovery) and 124 were used to evaluate depth of migration. Four RDSTs were unusable due to a malfunctioning pressure sensor or improper tag set-up. The majority of the fish tagged with RDSTs (74%) were recaptured at the Lower Granite Dam adult fish trap and provided an extensive history of the fish's migration depth through the lower Columbia and Snake rivers. Based on last telemetry records of fish at fixed receiver sites, 61% of the unaccounted-for fish were last detected upstream of Priest Rapids Dam (rkm 638.9), 23% in the lower Columbia River downstream of John Day Dam (rkm 346.9), and 16% in the Columbia River between Priest Rapids and John Day dams (Table 1).

The median depth of most individuals migrating through lower Columbia and Snake rivers was deeper than 2-3 m (Figure 4). Median migration depths of adult springsummer Chinook salmon were significantly deeper at Bonneville and The Dalles reservoirs than at upstream reservoirs (repeated measures ANOVA, df = 6, 106, F = 48.2, P < 0.0001, Figure 5). Median depths at lower Columbia River dam tailraces were deepest at Bonneville Dam and shallowest at Ice Harbor Dam (repeated measures ANOVA, df = 7, 149, F = 20.7, P < 0.0001; Figure 6). Interestingly, there was a significant effect of subject (=fish) in the repeated measures test for Chinook salmon, indicating the depth use of individual fish was consistent among reservoirs (i.e. some fish consistently used relatively deep water while others used relatively shallow water). The relationship between the dissolved gas saturation of the water and the fish's median depth were significant (P < 0.05), but weak (largest r² value = 0.097) at some locations (Bonneville, John Day Ice Harbor, and Little Goose reservoirs) but not others (The Dalles, McNary, and Lower Monumental reservoirs; Figure 7).

Recapture			Recapture		
Location	Number	RKM	Location	Number	RKM
Lower Granite Dam	92	694.6	The Dalles	1	308.0-
Adult Trap			Reservoir		346.8
Bonneville Reservoir	15	235.2-	Hood River	1	272.6
		308.0			
John Day Reservoir	3	346.8-	Rocky Reach	1	762.2
		369.7	Dam		
Chief Joseph Dam	3	877.1	Similkameen	1	977.6
			River		
Salmon River	3	824.5	Clearwater River	1	745.8
Deschutes River	2	328.4	Unknown	1	

Table 1. Recapture location for adult spring-summer Chinook salmon tagged with RDSTs in 2002.



Figure 4. Median migration depths (bars) and one standard deviations (whiskers) for adult Chinook salmon migrating through lower Columbia and Snake River reservoirs during 2002.



Figure 5. Mean (cross in boxes), median (horizontal line in boxes), quartiles (lower and upper bound of boxes), 5th and 95th percentiles (solid circles), and 10th and 90th percentiles (dash ends of vertical line) of median migration depths for adult Chinook salmon during migration through the four lower Columbia and three lower Snake River reservoirs in 2002 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, and GO = Little Goose). Medians significantly different at P = 0.05 indicated by different letters (Tukey's *post hoc* test).



Figure 6. Mean (cross in boxes), median (horizontal line in boxes), quartiles (lower and upper bound of boxes), 5^{th} and 95^{th} percentiles (solid circles), and 10^{th} and 90^{th} percentiles (dash ends of vertical line) of median migration depths for adult Chinook salmon during migration through the four lower Columbia and four lower Snake River tailraces in 2002 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, and GR = Lower Granite). Medians significantly different at P = 0.05 indicated by different letters (Tukey's *post hoc* test).



Figure 7. Relationship between the total dissolved gas concentration of the water and the median depth of adult Chinook salmon migrating through lower Columbia and Snake River reservoirs in 2002.

Adult Chinook salmon swam at depths deeper than 2 m a majority of the time when migrating through reservoirs 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 72.7 % at Lower Monumental to 90.2 % at Bonneville (Figure 8). Fish were deeper than 1 m (providing at least 10% hydrostatic pressure compensation) ranging from 92.3 % of the time in the Little Goose Reservoir to 97.5 % of the time in the Bonneville Reservoir (Figure 8). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 2 m in the water column was significant though weak for Bonneville (linear regression, df = 121, P < 0.001, r² = 0.12), The Dalles (df = 108, P = 0.01, r² = 0.06) and Ice Harbor (df = 92, P = 0.04, r² = 0.05) reservoirs (Figure 9). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 1 m in the water column was significant though weak for Bonneville (linear regression, df = 121, P = 0.002, r² = 0.07) and The Dalles (df = 108, P = 0.03, r² = 0.04; Figure 9) reservoirs.

Adult spring-summer Chinook salmon generally migrated deeper in tailraces than in reservoirs. The percentage of time spent at least 2 m below the surface during migration through a tailrace ranged from 76.1% at Ice Harbor to 95.1 % at Bonneville (Figure 8). The percentage of time deeper than 1 m ranged from 94.7 % in the Lower Granite tailrace to 99.4% in The Dalles tailrace (Figure 8). These depths imply near continuous hydrostatic compensation.

Adult spring-summer Chinook salmon frequently altered their depth in the water column. The duration of time adult Chinook salmon typically occupied surface waters ranged from minutes at a time at depths < 2 m to seconds at depths < 1 m (Figures 10 and 11). Although durations of time near the surface were short but we found that adult spring-summer Chinook salmon frequently re-ascended to surface waters typically spending less than 60 min at a time at depths deeper than 2 meters before re-ascending to surface waters less than 2 m (Figures 11). The average duration of time spent at depths deeper than 1 m ranged anywhere from less than an hour to several hours (Bonneville and The Dalles reservoirs; Figure 10). The longest duration of time a fish was observed at a

depth less than 2 m was 18 hrs (Bonneville Reservoir) and the longest duration of time at a depth less than 1 m was 4.1 hours (The Dalles Reservoir; Figure 12).

Regressions of swimming depth versus the dissolved gas concentration of the water revealed significant, but weak increases in depth with increasing TDG at some locations but not others. Significant but weak negative relations existed between the average continuous time < 2 m in the water column and the dissolved gas saturation of the water in the Bonneville (linear regression, df = 121, F = 17.6, P < 0.0001, r² = 0.13), The Dalles (df = 108, F = 4.2, P = 0.04, r² = 0.04), John Day (df = 98, F = 4.7, P = 0.05, r² = 0.03) and Little Goose reservoirs (df = 90, F = 5.7, P = 0.02, r² = 0.06). No significant relationships were observed between dissolved gas levels and the average continuous time fish spent shallower than 1 m in the water column during migration through a reservoir.







Figure 8. Percentage of time spent between the surface and > 2 m by adult springsummer Chinook salmon tagged with radio data storage tags (RDSTs) during migration through tailraces (top) and reservoirs (bottom) of the Columbia and Snake rivers in 2002. Bars represent the percentage of time (pooled for all fish) spent at a given depth.



Figure 9. Relationship between the total dissolved gas concentration of the water and the percent of time adult Chinook salmon spend in the upper 2 meters of the water column during migration through lower Columbia and Snake River reservoirs in 2002.



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

Figure 10. Average time observed by adult Chinook salmon at depths shallower than 1 m (top panel) and deeper than 1 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 122), TD = The Dalles (n = 109), JD = John Day (n = 100), MN = McNary (n = 100), IH = Ice Harbor (n = 93), LM = Lower Monumental (n = 93), and GO = Little Goose (n = 91).



Figure 11. Average time observed by adult Chinook salmon at depths shallower than 2 m (top panel) and deeper than 2 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 122), TD = The Dalles (n = 109), JD = John Day (n = 100), MN = McNary (n = 100), IH = Ice Harbor (n = 93), LM = Lower Monumental (n = 93), and GO = Little Goose (n = 91).



Figure 12. Maximum time observed by adult Chinook salmon at depths shallower than 1 m (top panel) and 2 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 122), TD = The Dalles (n = 109), JD = John Day (n = 100), MN = McNary (n = 100), IH = Ice Harbor (n = 93), LM = Lower Monumental (n = 93), and GO = Little Goose (n = 91).

Steelhead

Of the 231 adult steelhead tagged with RDSTs, 178 tags were recovered (77% recovery) and 170 were used to evaluate depth of migration. Eight RDSTs were unusable due to a malfunctioning pressure sensor or radio, improper tag set-up, or insufficient telemetry records. Of the 170 RDSTs used to evaluated migration depth 125 tags were recaptured at the adult trap at Lower Granite Dam (Table 2). Based on last telemetry records of fish at fixed receiver sites, 43% of unaccounted-for fish were detected last upstream of Priest Rapids or Lower Granite dams, 32% in the lower Columbia River downstream of John Day Dam, and 25% between Priest Rapids or Lower Granite dams and John Day Dam (Table 2).

The median depth of most individuals migrating through lower Columbia and Snake reservoirs and dam tailraces were deeper than 2-3 m (Figure 13). Median migration depths of adult steelhead were generally deeper in the lower Columbia River reservoirs compared to lower Snake River reservoirs (repeated measures ANOVA df = 6, 23.1, F = 11.5, P < 0.001, Figure 14). Median depths at lower Columbia River dam tailraces were deepest at McNary Dam and shallowest at Lower Granite Dam (repeated measures ANOVA, df = 7, 328, F = 7.83, P < 0.0001; Figure 15).

The relationship between the dissolved gas saturation of the water and the fish's median depth was significant (P < 0.05) in the McNary Reservoir ($r^2 = 0.23$) and Ice Harbor Reservoir ($r^2 = 0.375$; Figure 16). Median migration depths were significantly deeper in Bonneville Reservoir (Mann-Whitney Test, Z = -4.02, P < 0.001) during the spill season (Figure 17). No significant relationship existed between in the median depth of migration between spill seasons in The Dalles, John Day, and McNary reservoirs (Mann-Whitney Test, P > 0.05; Figure 17). Comparisons were not made for Ice Harbor, Little Goose, and Lower Monumental reservoirs because of insufficient depth data during the spill season.

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Recapture Location	Number	RKM	Recapture Location	Number	RKM
Lower Granite Dam	125	694.6	Below Bonneville	1	<235.1
Adult Trap			Dam		
Bonneville Reservoir	18	235.5-	Methow River	1	843.0
		308.0			
John Day Reservoir	4	346.8-	Clearwater River	1	745.8
		369.7			
Klickitat River	4	290.3	Salmon River	1	824.5
Snake River	4	521.6	Wells Dam	1	829.6
The Dalles Reservoir	3	308.0-	Unknown	5	
		346.8			
Lochsa River	2	902.8			

Table 2. Recapture location for adult steelhead tagged with RDSTs in 2002.



Figure 13. Median migration depths (bars) and one standard deviations (whiskers) for adult steelhead migrating through lower Columbia and Snake River reservoirs during 2002.



Figure 14. Mean (cross in boxes), median (horizontal line in boxes), quartiles (lower and upper bound of boxes), 5th and 95th percentiles (solid circles), and 10th and 90th percentiles (dash ends of vertical line) of median migration depths for adult steelhead during migration through the four lower Columbia and three lower Snake River reservoirs in 2002 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, and GO = Little Goose). Medians significantly different at P = 0.05 indicated by different letters (Tukey's *post hoc* test).



Figure 15. Mean (cross in boxes), median (horizontal line in boxes), quartiles (lower and upper bound of boxes), 5th and 95th percentiles (solid circles), and 10th and 90th percentiles (dash ends of vertical line) of median migration depths for adult steelhead during migration through the four lower Columbia and four lower Snake River tailraces in 2002 (BO = Bonneville, TD = The Dalles, JD = John Day, MN = McNary, IH = Ice Harbor, LM = Lower Monumental, GO = Little Goose, and GR = Lower Granite). Medians significantly different at P = 0.05 indicated by different letters (Tukey's *post hoc* test).



Figure 16. Relationship between the total dissolved gas concentration of the water and the median depth of adult steelhead migrating through lower Columbia and Snake River reservoirs in 2002.



Figure 17. Mean (cross in boxes), median (horizontal line in boxes), quartiles (lower and upper bound of boxes), 5th and 95th percentiles (solid circles), and 10th and 90th percentiles (dash ends of vertical line) of median migration depths for adult steelhead in the four lower Columbia River reservoirs in 2002 during spill and no spill conditions. Depth data is not available for adult steelhead migrations at Ice Harbor, Lower Monumental, and Little Goose reservoirs during the spill season. Comparisons where made using a Mann-Whitney test.

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 65.2% at Little Goose to 88.6% at Bonneville (Figure 18). Fish were deeper than 1 m (providing at least 10% hydrostatic pressure compensation) ranging from 86.5% of the time in the Lower Monumental Reservoir to 97.1 % of time in The Dalles Reservoir (Figure 18). The percentage of time spent at least 2 m below the surface during migration through a dam tailrace ranged from 62.9% at Bonneville to 93.8% at Ice Harbor (Figure 18). The percentage of time deeper than 1 m ranged from 78.9% in the Bonneville tailrace to 99.5% in the tailrace of Ice Harbor Dam (Figure 18). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 2 m in the water column was significant though weak for Bonneville (linear regression, $df 166 = , P = 0.0002, r^2 = 0.08$, The Dalles ($df 117 = , P = 0.01, r^2 = 0.05$) and Ice Harbor ($df 61 = , P = 0.01, r^2 = 0.10$) reservoirs (Figure 19). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 1 m in the water column was significant though weak for Bonneville (linear regression, $df 166 = , P = 0.001, r^2 = 0.10$), reservoirs (Figure 19). The relationship between the dissolved gas saturation of the water and the percentage of time fish were deeper than 1 m in the water column was significant though weak for Bonneville (linear regression, $df 166 = , P < 0.001, r^2 = 0.10$), The Dalles ($df 117 = , P = 0.02, r^2 = 0.05$; Figure 19) and John Day ($df = 63, P = 0.04, r^2 = 0.06$) reservoirs (Figure 19).

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 (Figures 20-21). Although durations of time near the surface were typically short, we found that adult steelhead frequently reascended to surface waters. Steelhead generally spent less than 30 min at a time at depths deeper than 2 m before re-ascending to surface waters. The median duration of time deeper than 2 m deep in the water column before re-ascending to a depth shallower than 2 m ranged from 7.3 min (Bonneville Reservoir) to 1.7 min (Ice Harbor Reservoir; Figure 21). The median duration of time deeper than 1 m in the water column before reascending to a depth shallower than 1 m ranged from 1.4 hrs (Bonneville Reservoir) to 4.2 min (Ice Harbor Reservoir; Figure 20). However, some fish were observed spending several consecutive days at depths shallower than 1 and 2 m (Figure 22). The maximum successive time < 1 and < 2 m observed by an individual fish outfitted with a RDST was 22 d and 24 d, respectively (Figure 22).

Regressions of swimming depth versus the dissolved gas concentration of the water revealed significant, but weak increases in depth with increasing TDG at some locations but not others (Figure 23). Significant but weak negative relations existed between the average continuous time < 2 m in the water column and the dissolved gas saturation of the water in the Bonneville (linear regression, df = 166, F = 9.7, P = 0.002, r² = 0.06) and Little Goose reservoirs (df = 33, F = 8.2, P = 0.007, r² = 0.20). No significant relationships were observed between dissolved gas levels and the average continuous time fish spent shallower than 1 m in the water column during migration through a reservoir (Figure 23).





Columbia and Snake River Reservoirs



Figure 18. 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) and reservoirs (bottom) of the Columbia and Snake rivers in 2002. Bars represent the percentage of time (pooled for all fish) spent at a given depth.



Figure 19. Relationship between the total dissolved gas concentration of the water and the percent of time adult steelhead spend in the upper 2 meters of the water column during migration through lower Columbia and Snake River reservoirs in 2002.



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

Figure 20. Average time observed by adult steelhead at depths shallower than 1 m (top panel) and deeper than 1 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 167), TD = The Dalles (n = 118), JD = John Day (n = 89), MN = McNary (n = 75), IH = Ice Harbor (n = 62), LM = Lower Monumental (n = 59), and GO = Little Goose (n = 54).



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

Figure 21. Average time observed by adult steelhead at depths shallower than 2 m (top panel) and deeper than 2 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 167), TD = The Dalles (n = 118), JD = John Day (n = 89), MN = McNary (n = 75), IH = Ice Harbor (n = 62), LM = Lower Monumental (n = 59), and GO = Little Goose (n = 54).



Figure 22. Maximum time observed by adult steelhead at depths shallower than 1 m (top panel) and 2 m (bottom panel) during migration through the four lower Columbia and three lower Snake River reservoirs in 2002. BO = Bonneville (n = 167), TD = The Dalles (n = 118), JD = John Day (n = 89), MN = McNary (n = 75), IH = Ice Harbor (n = 62), LM = Lower Monumental (n = 59), and GO = Little Goose (n = 54).



Figure 23. Relationship between the total dissolved gas concentration of the water and the duration of time steelhead spend in the upper 2 m of the water column during migration through lower Columbia and Snake River reservoirs in 2002. Note y-axis scales are different.

Discussion

We found that adult Chinook salmon and 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. Behavior was similar to those fish that were tagged with RDSTs in 2000 as were the TDGS levels in-river, which were at or slightly below long-term averages The observed depth-use of adult Chinook salmon and steelhead may explain the relatively low incidence of GBD observed in adults sampled at Bonneville Dam between 1995-1999 when gas supersaturation levels were typically lower than 120-125% (Backman and Evans 2002).

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 Chinook salmon and steelhead could potentially be exposed to gas supersaturated water for long periods of time (Keefer 2004a). However, although Chinook salmon and 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 Chinook salmon and 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; 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 involves 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 (10m) aquarium and no mortality was observed within 7 d at total dissolved gas levels of 130% (Dawley et al. 1975).

The short periods spent near the surface followed by return dives to deeper (> 2 m) 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, fall Chinook salmon and steelhead tagged in late summer when average TDGS were < 105% exhibited qualitatively identical patterns of frequent and rapid depth changes (Johnson et al. in review, C. Caudill unpublished data). Alternatively, adult Chinook salmon and 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. Upstream migration is energetically demanding, requiring 50-70% of initial energy reserves, and thus it may be energetically unfeasible for fish to actively search for water with lower TDG concentrations (Brett 1995; Pinson 2005). Similarly, Chinook salmon and steelhead may not have the sensory capabilities to recognize supersaturated water since high saturation levels and selection for avoidance behavior has been historically absent. Gas supersaturation occurs at natural channel constrictions such as waterfall (e.g. Celilo Falls on the Columbia River, currently inundated by The Dalles Dam). The lack of a response to supersaturated water conditions by adults suggests a lack of past selection for gas supersaturation avoidance, perhaps because saturation levels at natural cataracts rarely exceeded 115% and / or swimming depth provided adequate hydrostatic compensation for historic levels of TDG associated with waterfalls.

Explanations for the apparent lack of vertical avoidance could reflect a searching behavior. In open water salmon and steelhead 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 fish to continuously change 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 near the surface. Such behavior could explain the continuous up and down movements in the water column that we observed. Continuous vertical movements in the water column were also observed in adult Chinook salmon and steelhead during 2000 (Johnson et al. 2005; Johnson et al. in review).

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 (i.e. in the Columbia River immediately downstream of a tributary) where gas saturation levels would be near normally saturated i.e. 100-105% TDGS (Johnson et al. in review). The average continuous time recorded by an adult Chinook salmon and steelhead at depths shallower than 1 and 2 m would probably be insufficient to affect reproductive success or cause severe GBD symptoms or mortality based on in-river dissolved gas levels in 2002. 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.

The level of supersaturation that fish can safely tolerate varies depending on species, body size, exposure duration, general physical condition, swimming depth, and water

temperatures, which, affects the solubility of dissolved gases (Ebel et al. 1975; Weitkamp and Katz 1980). Backman and Evans (2002) observed higher GBD prevalence in steelhead than Chinook salmon sampled at Bonneville Dam. We observed steelhead spending a higher proportion of time near the waters surface downstream of Bonneville Dam (~ 20% of total time at depths shallower than 1 m) compared to Chinook salmon (< 1% of total time at depths shallower than 1 m). Other factors for these differences in GBD between species could be the related to the timing and speed of migration (Backman and Evans 2002) or tolerance to supersaturated water (Dawley and Ebel 1975; Weitkamp and Katz 1980; Mesa et al. 2000)

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 reabsorption (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 levels 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 (Figure 23). Migrating deeper in the late summer and early fall also could be a response to increased water temperatures as the thermocline deepens.

The conclusion that effects of TDGS are minimal for adult Chinook salmon and steelhead migrants in the Columbia and Snake rivers assumes that gas levels in the study were representative and that our sample was not biased. Our study years did not encompass the entire range of potential dissolved gas exposure levels in the system. Dissolved gas conditions during 2002 were typically at or slightly lower than the 10-year average at most hydroelectric projects, rarely exceeding 125% TDGS. Supersaturated conditions are generally higher in years with high river discharge and high levels of uncontrolled spill (e.g. 1997), and during high discharge years, hydrostatic compensation may be insufficient to prevent physiological effects from exposure to supersaturated conditions. There was a potential for GBD or other gas supersaturated-related mortality to bias our sample because the RDSTs had to be recovered. Any fish that made shallow migrations and died as a result of TDG exposure would have been lost from the sample. However, detailed analysis of telemetry records throughout the basis revealed that most unrecovered transmitters were detected last 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 of the unaccounted-for fish, 23% (Chinook salmon) and 32% (steelhead) were last detected in the lower Columbia downstream of John Day Dam where transmitter regurgitation rates were highest (Keefer et al. 2004b). Among these fish there was no apparent increase in loss rates during the periods of the highest TDGS. Hence there appeared to be little potential for bias in tag recovery to qualitatively bias our results here.

Summary

Evaluation of adult Chinook salmon and 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) in-river. We caution that greater TDGS and behavioral responses may occur in years with higher discharge and spill conditions. 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% for extended periods of time (Beiningen and Ebel 1970). However, 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. 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 recorded. The apparent vertical movement into and out of the surface layers by adult Chinook salmon and 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 potential.

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