ESTIMATING ADULT CHINOOK SALMON EXPOSURE TO DISSOLVED GAS
SUPERSATURATION DOWNSTREAM OF HYDROELECTRIC DAMS USING
TELEMETRY AND HYDRODYNAMIC MODELS

ERIC L. JOHNSON, a, TAMI S. CLABOUGH, a CHRISTOPHER A. PEERY, a DAVID H. BENNETT, b
THEODORE C. BJORNN, a, CHRISTOPHER C. CAUDILL, a and MARSHALL C. RICHMOND c

a Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844-1141, USA
b Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho 83844, USA
c Pacific Northwest National Laboratory, P.O. Box 999, MS K9-36, Richland, Washington 99352, USA

ABSTRACT

Gas bubble disease (GBD) has been recognized as a potential problem for fishes in the Columbia River basin. GBD results from exposure to gas supersaturated water created by discharge over dam spillways. Spill creates a downstream plume of water with high total dissolved gas supersaturation (TDGS) that may be positioned along either shore or mid-channel, depending on dam operations. We obtained spatial data on fish migration paths and migration depths for adult spring and summer Chinook salmon, Oncorhynchus tshawytscha, during 2000. Migration paths were compared to output from a two-dimensional (2-dimensional) hydrodynamic and dissolved gas model to estimate the potential for GBD expression and to test for behavioural avoidance of the high TDGS plume. We observed salmon swam sufficiently deep in the water column to receive complete hydrostatic compensation 95.9% of the time spent in the Bonneville Dam tailrace and 88.1% of the time in the Ice Harbor Dam tailrace. The majority of depth uncompensated exposure occurred at TDGS levels >115%. Adult Chinook salmon tended to migrate near the shoreline and they tended to remain in relatively deep water. Adults moved into the high dissolved-gas plume as often as they moved out of it downstream of Bonneville Dam, providing no evidence that adults moved laterally to avoid areas with elevated dissolved gas levels. When water depths decreased due to reduced river discharge, adults tended to migrate in the deeper navigation channel downstream from Ice Harbor Dam. The strong influence of dam operations on the position of the high-TDGS plume and shoreline-orientation behaviours of adults suggest that exposure of adult salmonids to high-TDGS conditions may be minimized using operational conditions that direct the spilled water mid-channel. Our approach illustrates the potential for combined field and modelling efforts to estimate the fine-scale environmental conditions encountered by fishes in natural and regulated rivers. Published in 2007 by John Wiley & Sons, Ltd.

KEY WORDS: fish behaviour; gas bubble disease; hydrologic modelling; Chinook salmon; fish depth; gas supersaturation

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INTRODUCTION

The impacts of main stem 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 dramatic effect of dams on river conditions is the elevated levels of dissolved gas caused by the entrainment of atmospheric gases as water passes over spillways. Since the early 1990s, voluntarily spilling water over dam spillways has been one management effort 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 (Scholmen 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 the evening and night 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 supersaturation conditions that exceed the water quality standard of 110% total dissolved gas supersaturation (TDGS). Voluntary spill has raised concern about the effects of exposure to supersaturated dissolved gas levels on adult spring and summer Chinook salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss* because the spill period coincides with their upstream migration timing.

Most of the 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 aquatic organisms, particularly free-swimming adult salmonids, since depth-use by individual fish strongly influences the biological effects of TDGS. The formation of interstitial gas bubbles in tissues and subsequent expression of gas bubble disease (GBD) is the best known physiological effect of exposure to high TDGS and has been known to cause potentially lethal vascular and cardiac blockage or haemorrhaging in addition to increasing a fish’s susceptibility to disease and predation, and reducing growth and swimming performance (Dawley and Ebel, 1975). Expression of GBD in adult salmonids held in shallow water (less than 1 m) typically begins at TDGS levels between 110 and 120% (Rucker and Tuttle, 1948; Westgard, 1964; Wood, 1968), levels frequently recorded in the Columbia and Snake rivers.

Under field conditions, the high degree of spatial and temporal variations in dissolved gas saturations downstream of dams could also result in different exposure levels for individual fish using different paths of migration (Scheibe and Richmond, 2002). The effects of TDGS are largely determined by both the dissolved gas concentration of the water and the depth of the fish. While the concentration of dissolved gasses remains relatively constant with depth, per cent saturation determines whether interstitial gas bubbles form and is strongly affected by pressure. At a given TDG concentration, hydrostatic pressure reduces the effective TDG level by about 10% of saturation per meter of depth. A fish maintaining a constant depth of 2 m in water saturated at 120% would experience complete hydrostatic compensation, whereas, a fish maintaining a depth of 1 m would experience partial compensation. In addition to TDGS and fish depth, the effects from TDG exposure can vary depending on species, body size, physical condition, interindividual susceptibility, location of emboli formation, fish activity and water temperature (Weitkamp and Katz, 1980; Hans *et al*., 1999; Mesa *et al*., 2000; Morris *et al*., 2003). While the relationship between fish depth and GBD is relatively well understood, how fish respond to horizontal variability in TDG and how this variability affects TDG exposure has not been studied. TDG concentrations downstream of dams are variable because discharge from the spillway forms a distinct plume with much greater TDG than water passed through turbines. The position of the plume may be against one shore or the other or mid-river, depending on spill levels and dam operations (Richmond *et al*., 1999).

In a previous study (Johnson *et al*., 2005) we estimated the potential for TDG exposure using depth data from individual fish and point sampling of TDG at dams. Here, we extend those analyses to estimate how smaller scale spatial and temporal variations in TDG interact with fish migration behaviour to determine the potential for gas bubble formation in tissues. We combined model data on spatial variability in TDG levels below dams (Perkins and Richmond, 2004a, 2004b) with three-dimensional (3-dimensional) positioning of individual fish as they approached dams to estimate TDG exposure. In particular, we were interested in the position of fish in relation to the high-TDGS plume. The objectives for this study were to (1) estimate TDG exposure in two reaches with spatial and temporal variability in dissolved gases saturations using data on the migration path and depth by individual fish obtained by telemetry in conjunction with output from a high resolution hydrological model and (2) determine migration paths of adult spring and summer Chinook salmon relative to water with higher dissolved gas concentrations as a test of whether fish avoid supersaturated conditions. We focused on reaches downstream of Bonneville and Ice Harbor dams where horizontal gradients of dissolved gas were known to occur (Scheibe and Richmond, 2002).

### STUDY SITE

A large part of the main stems of the Columbia and Snake rivers consist of a series of reservoirs created by hydroelectric dams. This study was conducted in two reaches immediately downstream of dams where temporal...
and spatial gradients of dissolved gas occur as a result of water spilling over the dam spillways. The first reach was on the Columbia River downstream of Bonneville Dam, the first dam adult salmonids encounter during their upstream migration from the Pacific Ocean (Figure 1). Radio-tagged adult Chinook salmon were tracked by boat from release sites (Dodson, OR and Skamania, WA) at river kilometre (RKM) 225.6 (measuring from the mouth of the Columbia River) 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, 1991). The banks downstream of Bonneville Dam are steep and rocky. Point estimates of TDG levels recorded by a monitoring station downstream of Bonneville Dam during 2000 were similar to the 10-year average ranging from 110 to 120% TDGS during the spill season (Figure 2).

The second reach was on the lower Snake River immediately downstream of Ice Harbor Dam (Figure 1). Radio-tagged fish were tracked from the Snake River mouth (RKM 521.6) upstream to Ice Harbor Dam (RKM 537.7). From the Snake River mouth upstream approximately 8 km to Strawberry Island the narrow shipping channel is located mid-river and runs adjacent to the south shore of Strawberry Island. Upstream of Strawberry

Figure 1. The Columbia and Snake rivers study area where the migration of radio-tagged adult spring and summer Chinook salmon was monitored during 2000 (enlarged areas indicate reaches of intense boat tracking)
Island the river channel parallels the north shoreline. The depth of the river channel varies with location but is generally greater than 6 m. Water depths adjacent to the channel are shallower ranging from 1 to 3 m depending on dam discharge (Romar Books, 1991). The north bank in this section of river is steep and rocky, whereas the south bank rises gradually, forming several small islands. TDGS levels recorded by the monitoring station downstream of Ice Harbor Dam during the spill season were typically lower than the 10-year average, ranging from 107 to 120% TDGS (Figure 2).

**METHODS**

*Tagging procedures*

Adult Chinook salmon were trapped and tagged from 4 April to 31 July 2000 at the Bonneville Dam adult fish facility located adjacent to the Washington-shore fishway. A total of 1132 adult spring and summer Chinook salmon were tagged for multiple study objectives (e.g. Keefer *et al.*, 2004; Johnson *et al.*, 2005). Fish were tagged...
intragastrically (through the mouth into stomach) with either a 7 V (8 × 1.6 cm; 29 g in air) standard radio transmitter or a 3 V (9 × 2 cm; 34 g in air) radio data storage transmitter (RDST; Lotek Wireless, Inc., Newmarket, Ontario). Radio data storage transmitters were programmed to record pressure at 5-s intervals during upstream migration, which allowed approximately 40 days of data storage. Estimated accuracy of the pressure sensor in the RDST was 4.8 kPa (0.5 m, Lotek Wireless, Inc.). These transmitters were placed in 228 spring and summer Chinook salmon thought to be of Snake River origin based on passive integrated transponder (PIT) tag codes and adipose fin clips, so that tags could be recovered at a fish trap at Lower Granite Dam (RKM 695; Harmon, 2003). After tagging fish were moved to a 2275-L oxygenated tank full of river water where they were held (average 1.5 h; range 0.5–6.0 h), until transported downstream by truck, and released. Following recovery, fish were released at two locations downstream of Bonneville Dam, Dodson Landing (RKM 225.6) on the Oregon shore or Skamania Landing (RKM 224.5) on the Washington shore in approximately equal proportions. We attempted to intensively track only one to two fish at a time, substantially reducing the total number of fish tracked. Fish typically began to move upstream within 20–30 min of release. Upon release of a group of radio-tagged fish, tracking priority was given to fish with RDST’s (identified by channel and code); of those fish, whichever recommenced migration first was tracked. We were unable to directly assess the effects of tagging and transport on fish behaviour. However, Matter and Sandford, (2003) compared migration behaviour in PIT- and radio-tagged Chinook salmon using data from the same study year and found no evidence of biologically significant differences in migration rate. More details on tagging methods and operation of the Bonneville Dam adult fish facility can be found in Keefer et al. (2004).

Migration routes

Individual fish migration routes were determined by tracking individual fish daily using boats equipped with six-element directional antennas and Lotek SRX400 radio receivers to track fish downstream of Bonneville and Ice Harbor dams from mid-April to September. Fish locations were determined by orienting the fish between the boat and the nearest shoreline using the directional antenna and approaching the shoreline until the highest power reading was recorded on the SRX receiver. Based on previous studies locating fixed tags in the water, the estimated accuracy of fish positions was 0–20 m. Tagged fish were tracked from the release sites to the boat-restricted zone just downstream of Bonneville Dam, and from the Snake River confluence to the boat-restricted zone just downstream of Ice Harbor Dam. If the fish were tracked less than half the distance through the tailrace, they were excluded from the analysis. Tracking typically consisted of locating fish every 10–20 min during daylight hours as they progressed through the tailrace reaches; in some cases we inferred paths for up to several kilometres assuming straight-line paths when fish locations were temporarily lost, for example, when fish sounded deeply as they crossed the river channel. Transmitter channel, code, location, date, time and tracking routes were recorded on Geographic Information Systems (GIS) maps of each area.

Logistic regression analysis was used to evaluate associations between the release locations, positions of dissolved-gas plumes and fish migration paths using the model:

\[ \text{Logit} \{ \Pr(Y = 1) \} = \beta_0 + \beta_1 \text{(release site)} + \beta_2 \text{(gas plume location)} + \beta_3 \text{(release site × plume location)} \]

where,

- \( Y \) denotes river crossing status (1 = fish crossed, 2 = fish did not cross river)
- Release site (1 = Dodson, OR or 2 = Skamania, WA)
- Gas Plume location = (Same side as fish, mid-river or opposite side as fish).

Hydrodynamic and dissolved gas modelling

Depth-averaged water velocities, dissolved gas saturation and water temperature downstream of the Bonneville and Ice Harbor dams were simulated using the hydrodynamic and water quality model Modular Aquatic Simulation System 2-D (MASS2). MASS2 (Perkins and Richmond, 2004a, 2004b) is an unsteady, 2-dimensional, model that simulates hydrodynamics and water quality in rivers and estuaries for subcritical and supercritical flow regimes. The model uses a structured multi-block, curvilinear computational mesh to represent the river geometry. Finite-volume methods (Patankar, 1980) are used to solve the conservation equations for mass, momentum and water quality constituents. The model is computationally efficient; it has been used to simulate flow conditions over long reaches (25–125 km) at high spatial resolution (cells sizes are typically 5–50 m) and high temporal resolution.
(on the order of 30 s time steps). MASS2 has been used in several applications on the Columbia and Snake River systems. These studies include simulating dissolved gas transport (Richmond et al., 2000), time-varying salmon habitat and stranding caused by discharge fluctuations (Perkins et al., 2004), and radionuclide transport (Kincaid et al., 2000).

MASS2 validation simulations documented in Richmond et al. (1999) show that the model accurately represents the spatial and temporal distributions of the simulated quantities. Water surface elevations and velocities compared favourably with measured tailwater elevations at both dams and velocities measured using an acoustic Doppler current profiler (ADCP). Depending on the specific time and location the simulated dissolved gas saturations were observed to under- or over-predict compared to the values measured during field studies conducted in 1996 and 1997. In the Ice Harbor model about 90% of the simulated gas saturation values were within ±5% of the observations. For the Bonneville model, about 88% of the simulated gas saturation values were within ±5% of the observations.

Existing MASS2 models that were configured and validated for the U.S. Army Corps of Engineers (USACE) Dissolved Gas Abatement Study (DGAS) were used in this work (Richmond et al., 1999). The Ice Harbor and Bonneville tailrace reaches (Figure 1) were subsections of models that encompassed larger river reaches. The Ice Harbor model extended from Ice Harbor Dam downstream to McNary Dam (Figure 1) and consisted of 26 000 cells with an average size of 40 m. The Bonneville model covered the area from Bonneville Dam downstream to RKM 177 (upstream of the Willamette River) using a grid with 35 000 cells with an average size of 22 m. The boundary conditions required for MASS2 were river discharge (separated as spill and powerhouse generation discharge for boundaries at hydroelectric projects), water temperature and dissolved gas concentration at the upstream boundaries and water surface elevation (stage) at the downstream boundaries. Additional information about the boundary conditions is provided by Rakowski et al. (2003).

Output from MASS2 was used to estimate the dissolved gas concentrations experienced by RDST-tagged adult spring and summer Chinook salmon that were monitored in the Bonneville and Ice Harbor dam tailraces. Time-varying simulations were run for time periods each fish was tracked in the Bonneville and Ice Harbor tailraces. Simulations provided flow, velocity, water temperature and gas saturation information at approximately 30 m increments during a fish’s track. We assumed that dissolved gas concentrations did not vary vertically.

Exposure to TDGS after accounting for effects of hydrostatic pressure compensation was estimated using the depth of the fish from the RDSTs and the compensation depth (depth that provides complete hydrostatic pressure compensation) determined using total dissolved gas pressure estimated from the MASS2 model output:

\[
\text{Comp. depth (m)} = \left(\frac{\text{barometric pressure mmHg} - \text{TDG pressure mmHg}}{23}\right) \times 0.3048
\]

(U.S Army Corps of Engineers Technical Management Team Internet site; United States Army Corps of Engineers, 1998).

Degree of dissolved gas exposure accounting for hydrostatic compensation benefits was calculated using the following formula:

\[
\text{Degree of Exposure} (%) = \left(\frac{\text{compensation depth m} - \text{fish depth m}}{10}\right) \times 10 + 100.
\]

**RESULTS**

Of the 1132 adult spring and summer Chinook salmon that were released with radio transmitters downstream of Bonneville Dam during the study period, 72 salmon (35 with RDST and 37 with standard transmitters) were tracked sufficiently to summarize migratory routes relative to the position of the dissolved-gas plume downstream of Bonneville Dam. Tracking averaged 5h per fish in the Bonneville tailrace and 3.5h in the Ice Harbor tailrace. Typically one to two fish were tracked per day therefore only a subset of fish tagged with RDST were included in this analysis. The remaining RDST fish that were released but not tracked downstream of Bonneville or Ice Harbor dams were used to describe system-wide TDG exposure (Johnson et al., 2005). Of the tracked salmon, approximately equal proportions were released on the WA (51.4%) and OR shores (48.6%). Forty-nine adult spring and summer Chinook salmon (68% of the total tracked) were monitored migrating when the dissolved-gas plume was positioned mid-river, a condition that occurs during spill with approximately equal discharge from...
powerhouses 1 and 2 at Bonneville Dam (Figure 3). Thirteen fish (18%) were tracked when the dissolved-gas plume was located along the Washington shore, which occurs when the majority of discharge is from powerhouse 1 (Figure 4). Ten fish (14%) were tracked when the dissolved-gas plume was along the Oregon shore, with the majority of discharge from powerhouse 2 (Figure 5).

Downstream from Bonneville Dam, fish generally migrated in close proximity to the shoreline (usually within 50 m) with little time spent mid-river except when crossing between shorelines. The majority (58.3%) of adult spring and summer Chinook salmon did not cross the river from the shoreline of release. Among fish that crossed the river, we found neither an association between crossing events and release location (logistic regression, \( \chi^2 = 0.68, \text{df} = 1, p = 0.408 \)) nor between crossing events and the location of the dissolved-gas plume (logistic regression, \( \chi^2 = 0.36, \text{df} = 1, p = 0.547 \)). Approximately equal proportions of salmon crossed from the Washington shore to the Oregon shore (17 of 30 or 56.7%) as from the Oregon shore to the Washington shore (13 of 30 or 43.3%). A similar number of adults crossed the river into water with elevated gas levels (7 of 12 or 58%) as those leaving water with elevated gas levels (5 of 12 or 42%). The remaining 18 fish crossed when the TDG plume was in the middle of the river.
Generally, migration behaviour of fish in the Ice Harbor tailrace was similar to that observed downstream of Bonneville Dam with respect to near-shore orientation. Eighty-six (19 with RDSTs) spring and summer Chinook salmon were partially tracked from the confluence of the Snake River to Ice Harbor Dam. Fish observed migrating in the Ice Harbor tailrace after water levels dropped in mid to late June showed a strong tendency to migrate up the shipping channel along the north shore (71%). Migration routes were more evenly split between the north and south shorelines before water levels dropped (53% south shore and 47% north shore). Based on model simulations, the position of the dissolved-gas plume downstream of Bonneville Dam changed frequently throughout the day making it unfeasible to accurately determine if fish were avoiding the dissolved-gas plume at this location.

After accounting for compensation from fish depth, few fish were exposed to high TDGS levels. Depth and temperature data were retrieved from 35 adult spring and summer Chinook salmon mobile-tracked downstream of Bonneville Dam and from 19 salmon mobile-tracked downstream from Ice Harbor Dam. Data collected from RDSTs revealed that fish were deep enough in the water column to receive complete hydrostatic compensation 95.9% of time spent in the Bonneville tailrace and 88.1% of the time in the Ice Harbor tailrace based on dissolved
gas saturations estimated from MASS2 model simulations and corresponding fish locations and depth records (Figure 6). One per cent of the depth uncompensated exposure was equivalent to a level of dissolved gas supersaturation between 101 and 105%, 1.8% to a level between 106 and 110%, 0.8% to a level between 111 and 115% and 0.3% to a level between 116 and 120%. In the Ice Harbor tailrace, 11.6% of the depth uncompensated exposure was equivalent to a level of dissolved gas supersaturation between 101 and 105%, and 0.3% to a level between 106 and 110%.

Adult spring and summer Chinook salmon encountered water with total dissolved gas saturations greater than 115% for a relatively small proportion of time (20% at Bonneville and 15% at Ice Harbor; Figure 7). However, it was during these periods when fish were exposed to potentially harmful gas supersaturated conditions, once accounting for the effects of depth compensation (Figure 7). At higher dissolved gas saturations (between 125 and 130%), fish were exposed to supersaturated conditions 70.7% of the time after accounting for the effects of depth (Figure 7). At water saturation levels between 125 and 130% TDGS, 46.5% of the depth uncompensated exposure was equivalent to gas supersaturation levels between 101 and 110%, 43.1% to levels between 111 and 115% and 10.4% to levels between 116 and 120%.

DISCUSSION

The study reaches downstream of Bonneville and Ice Harbor dams were characterized by supersaturated gas conditions during nearly all of the study period. As dam operations varied, supersaturated conditions differed across the channel, providing the potential for migrating adult salmon to minimize exposure to supersaturated conditions by moving laterally in the river channel. Consistent with previous analyses (Johnson et al., 2005), our comparisons of adult Chinook salmon migration routes and depth-use to the finer-scale estimates of TDG concentrations from the MASS2 model suggested that adults frequently encountered the TDG plume, but swam at depths that provided adequate hydrostatic compensation. The apparent lack of negative effects from exposure to supersaturated conditions appeared to be primarily related to the passive (in the behavioural sense) effects of hydrostatic depth compensation rather than active behavioural avoidance of supersaturated conditions by alteration of horizontal or vertical position.

Figure 6. Relationship between the MASS2 modelled compensation depth relative to the observed depth of adult spring and summer Chinook salmon in the Bonneville Dam tailrace (top) and the Ice Harbor Dam tailrace (bottom). Horizontal line represents the compensation depth (depth where there is complete hydrostatic pressure compensation).
Figure 7. Percent of time fish were exposed to supersaturated conditions (after compensating for depth) relative to the dissolved gas concentration of the water.
vertical positioning. Below, we discuss these patterns and potential mechanisms in greater detail, and discuss management implications.

Model results of dissolved gas supersaturation relative to the migration depth of adult spring and summer Chinook salmon indicate that exposure to gas supersaturation once accounting for the effects of hydrostatic compensation was minimal (less than 12% of the total time in the tailraces) during 2000. Most of the exposure (after accounting for depth) was equivalent to a level ranging between 100 and 110% TDGS in the Bonneville tailrace and between 100 and 105% TDGS in the Ice Harbor tailrace. These levels are lower than those generally considered lethal for adult salmon held in shallow water for extended time periods (Nebeker, 1973; Ebel et al., 1975; Nebeker et al., 1976) or to affect reproductive success based on acute exposure. Gale et al. (2004) observed no effect on pre-spawning mortality or reproductive success for female Chinook salmon late in their maturation after continuous exposure to gas supersaturated water (46 h at 114% TDGS and 10 h at 125% TDGS in 0.5 m deep tanks) though they caution that some of their experiments had a small sample size.

Adult Chinook salmon were observed migrating in water with saturation levels less than 115% more than 80% of the time. This result is consistent with the overall TDG conditions during the study period (Figure 2) and the general lack of GBD expression among spring–summer Chinook below Bonneville Dam as assessed by Backman and Evans (2002). However, when saturation levels of the water exceed 115% we found an increase in exposure to supersaturated conditions after accounting for depth effects (e.g. Figure 7). Signs of GBD and mortality have been observed for adult Chinook salmon in the Columbia River when saturation levels ranged between 123 and 143% for extended periods of time (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 days. Although estimates of dissolved gas exposures of Chinook salmon during 2000 were lower than levels known to cause GBD and mortality, dissolved gas levels above 120–125% can occur in the Columbia and Snake rivers and extended exposure at these levels can be dangerous, particularly in shallow areas of the river where the ability to hydrostatically compensate is limited (e.g. areas downstream of McNary, Lower Monumental and Ice Harbor dams).

The higher proportion of exposure observed in the Ice Harbor tailrace probably was related to the shallow depth of the river downstream from Ice Harbor Dam. Shrank et al. (1997) observed that GBD was prevalent in resident juvenile non-salmonid fishes downstream from Ice Harbor Dam but was rare in other reaches of the Columbia and Snake rivers. Many fish were observed migrating through shallow backwater areas north of Pierce and Ives Islands downstream of Bonneville Dam. The MASS2 model did not include these areas because bathymetry data were not available; therefore, these areas could not be estimated by the model. However, backwater areas such as the Pierce and Ives Island complex likely had lower saturation levels (potentially 6–20% lower depending on spill volume) than the main channel due to the lack of gas exchange with supersaturated water from the main river channel (Shrank et al., 1997). Additionally, backwater areas have a higher potential for more rapid gas dissipation as a result of a larger surface-area to volume ratio and relatively high vertical mixing rates. Although we observed many fish traversing through these relatively shallow areas, our likelihood of underestimating overall dissolved gas exposure in upriver migrants was probably negligible. Overall, in-river dissolved gas conditions during this study were at or slightly below long-term averages (Figure 2).

Despite the presence of strong lateral gradients in dissolved gas concentrations across the river channel, our results provide no evidence that adult spring and summer Chinook salmon moved laterally to avoid higher dissolved gas concentrations (greater than 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 are in contrast 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) suggesting the potential for ontogenetic differences in susceptibility (e.g. Gale et al., 2004) and/or the ability to detect and avoid supersaturated conditions. Since we were unable to account for all the effects of hydrostatic compensation because we monitored the migration paths of unrestrained fish, making robust comparisons to laboratory studies where fish were confined to a shallow depth is difficult. Again, salmon migrating in areas of the river with elevated gas concentrations were not confined to surface waters and received adequate compensation most of the time due to their vertical position in the water column, a pattern that may explain, in part, the lack of horizontal avoidance. Based on a larger sample of fish tagged with RDSTs, we observed weak associations between the per cent and...
duration of time fish occupied depths near the surface and the dissolved gas concentrations, suggesting a lack of vertical avoidance behaviour (Johnson et al., 2005), in addition to the lack of horizontal avoidance behaviour reported here.

Adult Chinook salmon may not have been aware of existing gradients in TDG at the scale of the whole river, perhaps because efforts to search the main river channel 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, adults may not have the sensory capabilities to recognize supersaturated water since extremely high saturation levels and selection for avoidance behaviour may have been historically absent. Gas supersaturation occurs at natural channel constrictions such as waterfalls (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 may be related to searching behaviours during homing. 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 homestream odours (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 in surface waters. Such behaviour may explain the near continuous up and down movements in the water column that we observed (Johnson et al., 2005). Prolonged dives into the water column below the hydrostatic compensation depth may also provide an opportunity for the reabsorption of bubbles that may have begun to form from exposure to supersaturation at shallow depths (Elston et al., 1997).

Adult spring and summer Chinook salmon 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 salmon in large river systems (Bjornn et al., 2000; Hinch et al., 2002; Reischel and Bjornn, 2003; Hughes, 2004; Standen et al., 2004; Keefer et al., 2006). It has been hypothesized that orientation to shorelines may be an energy-conserving behaviour as fish seek pathways associated near river banks with slower water velocities, reducing drag and minimizing energy expenditure (Hinch and Rand, 2000; Standen et al., 2002). We observed that crossing the river by adult Chinook salmon was more frequent where the river constricted, where a tributary flowed into the river from the opposite shoreline, or where a shallow shelf extended into the river. Similar behaviour has been observed with adult pink (Oncorhynchus gorbuscha) and sockeye (Oncorhynchus nerka) in large rivers systems with diverse flow conditions and habitat features (Hinch et al., 2002; Standen et al., 2002). It has been suggested that small-scale hydraulic conditions may influence when fish move across the river, presumably in an attempt to locate water with lower velocities to conserve energy (Standen et al., 2002). Migrating close to shore also may position fish better to detect chemical cues from the natal tributary, thus reducing the likelihood of straying (Keefer et al., 2006) and potentially affecting individual shoreline switching behaviour.

The conclusion that effects of TDGS are minimal for adult Chinook salmon 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 year did not encompass the entire range of potential dissolved gas exposure levels in the system. Dissolved gas conditions during 2000 were typically at or slightly lower than the 10-year average at most of the 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). 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 basin revealed that most of the unrecovered transmitters had been implanted in fish of mid-Columbia River origin because most unaccounted for fish (58%) were last documented in the Columbia River upstream of Priest Rapids Dam (RKM 639). Telemetry records indicate that 31% of unaccounted for RDSTs were last detected in the lower Columbia River downstream of John Day Dam where fishing pressure and transmitter regurgitation rates are highest (Keefer et al., 2004). 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.

MANAGEMENT IMPLICATIONS

We did not observe strong associations between migration routes and the dissolved gas concentration of the water or between the gas concentration and depth-use. Consequently, adults do not appear to behaviourally compensate by seeking water with lower TDG concentrations. Rather, exposure to supersaturated conditions in adults appears to be determined primarily by river environmental conditions.

We observed that adult spring and summer Chinook salmon were strongly oriented to the shoreline during upstream migration. Therefore 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. Such changes would probably be most beneficial in years with high river discharge and high spill levels.

The degree of exposure that did occur based on the model estimates of TDGS and fish depth was generally less than reported levels known to cause signs of GBD and mortality for adult salmonids. However, when high dissolved gas levels (greater than 125–130%) were encountered, fish did not fully compensate by increasing their swimming depth. Occurrences of extreme TDG levels are likely lower than in the past because of modifications (addition of flow deflectors at spillways) and operational changes, although, high gas levels do occur in years with high river discharge and spill (e.g. 1997). During years with chronically high TDGS (greater than 115–120%) caused by operational or uncontrolled spill, managers should anticipate the potential for increased GBD and strive to alter dam operations to direct the spilled water mid-channel insomuch as possible.

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