Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2010) **76**, 1520–1528
doi:10.1111/j.1095-8649.2010.02578.x, available online at www.interscience.wiley.com

Migration depths of adult steelhead *Oncorhynchus mykiss* in relation to dissolved gas supersaturation in a regulated river system

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(Received 10 February 2009, Accepted 12 January 2010)

Adult steelhead *Oncorhynchus mykiss* tagged with archival transmitters primarily migrated through a large river corridor at depths >2 m interspersed with frequent but short (<5 min) periods closer to the surface. The recorded swimming depths and behaviours probably provided adequate hydrostatic compensation for the supersaturated dissolved gas conditions encountered and probably limited development of gas bubble disease (GBD). Results parallel those from a concurrent adult Chinook salmon *Oncorhynchus tshawytscha* study, except *O. mykiss* experienced greater seasonal variability and were more likely to have depth uncompensated supersaturation exposure in some dam tailraces, perhaps explaining the higher incidence of GBD in this species.

Key words: behaviour; data storage tags; gas bubble disease; hydrostatic compensation.

Elevated gas levels in water can cause a condition in fish known as gas bubble disease (GBD; Weitkamp & Katz, 1980). Fish depth plays a central role in the expression of GBD because hydrostatic pressure has a strong influence on the total dissolved gas supersaturation (TDGS) exposure for individual fishes. Specifically, the increased hydrostatic pressure associated with swimming deeper in the water column inhibits formation of interstitial gas bubbles. Significant bubble formation is believed to require periods of tens of minutes to hours of uncompensated exposure to supersaturated conditions. Intermittent periods of greater hydrostatic compensation caused by swimming at greater depth can reduce signs of the disease (Knittel *et al.*, 1980; Weitkamp & Katz, 1980).

High supersaturation levels have been reported in lakes, coastal waters, rivers and reservoirs and have affected numerous fisheries resources (Ramsey, 1962; Harvey, 1967; Crunkilton *et al.*, 1980; Gray *et al.*, 1983; Heggberget, 1984; Lutz, 1995). Supersaturated conditions are common below hydroelectric dams, particularly when

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river discharge is released over spillways. Water spilling over Columbia and Snake River dams (U.S.A., 46° N; 124° W) during the snowmelt freshet creates plumes of high dissolved gas that extend downstream from dam spillways and supersaturated conditions that do not equilibrate in reservoirs (Ebel, 1969; Johnson *et al.,* 2007; Urban *et al*., 2008). In this system, water is also released over spillways to improve juvenile salmonid survival by reducing the number of smolts passing dam turbines (Schoeneman *et al*., 1961; Muir *et al*., 2001). Spill operations, however, have raised concerns about effects of supersaturated gas on downstream resident fishes (Montgomery & Becker, 1980; Counihan *et al*., 1998; Weitkamp *et al*., 2003) and migrating anadromous fishes (Schoeneman *et al*., 1961; Weitkamp & Katz, 1980; Backman & Evans, 2002). Adult Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and steelhead *Oncorhynchus mykiss* (Walbaum) are among the most exposed migratory populations because the spring–summer spill season coincides with their upstream migration timing (Robards & Quinn, 2002; Keefer *et al*., 2004*a*).

The relationship between TDGS, swimming behaviour and GBD in adult fishes has rarely been assessed in field settings. Instead, most studies have addressed the effects of dissolved gas exposure on juvenile fishes in laboratories (Westgard, 1964; Knittel *et al*., 1980; Heggberget, 1984; Krise & Meade, 1988; Mesa *et al*., 2000). The objectives of this study were to (1) determine the migration depth of adult *O. mykiss* and (2) assess the potential for exposure to high TDGS and GBD expression past a series of dams and reservoirs during persistent supersaturated conditions.

The study area included *c*. 470 river kilometres (rkm) of the lower Columbia and lower Snake Rivers, which consists of a series of reservoirs created by eight hydroelectric dams from Bonneville Dam (235 rkm) to Lower Granite Dam (695 rkm). Gas supersaturated conditions often persist throughout the lower Columbia and Snake Rivers in spring and summer because low turbulence does not facilitate gas transfer back into the atmosphere.

A total of 410 adult *O. mykiss* were trapped and intragastrically tagged (through the mouth into stomach) with a radio data storage transmitter (RDST; 3V, 9 cm × 2 cm, 34 g in air; Lotek Wirless, Inc; www.lotek.com) in 2000 and 2002. The methods used to capture and radio-tag fish have been described in detail elsewhere (Matter & Sandford, 2003; Keefer *et al*., 2005). Briefly, fish were diverted from the Washington shore fish ladder at Bonneville Dam into a facility where they could be selected by species. Diverted fish were anaesthetized, sexed, measured for fork length (L_F) and inspected for the presence of fin clips indicating known hatchery origin. Fish recovered in a dark, 2275 l, oxygenated transport tank full of river water and were then randomly released at two locations downstream of Bonneville Dam: Skamania Landing (224·5 rkm) on the Washington shore and Dodson Landing (225·6 rkm) on the Oregon shore. RDSTs were programmed to record fish body temperature at 1 min intervals and pressure at 5 s intervals, allowing 40 days of data storage. Accuracy was ±4·8 kPa (0·5 m) for the pressure sensor and ±0·15° C for the temperature sensor (Lotek Wireless, Inc.). Transmitters were recovered by diverting adults at the Lower Granite Dam fish trap and from hatchery and fisheries returns. Anaesthetization, handling and tagging were conducted under oversight of federal and state agencies and the University of Idaho Animal Care and Use Committee. The effects of tagging procedures on fish behaviour are difficult to assess, though prior research in the study system has indicated little evidence of altered behaviour in radio-tagged adult salmonids (Matter & Sandford, 2003; Keefer *et al*., 2005).

Oncorhynchus mykiss movements were monitored using fixed radio receivers at all major tributaries and at eight dams in the lower Columbia and Snake Rivers (Keefer *et al*., 2004*b*; Johnson *et al*., 2005). Time fish spent in tributaries was excluded from analyses of supersaturated gas exposure times. Total dissolved gas levels were frequently supersaturated at all reservoir and tailrace monitoring sites located in dam tailraces and forebays ($n = 15$) from April to August and were near the 10 year average in both years. TDG levels at monitoring sites were generally 95–105% in March and April, and then rapidly increased during the spill season to mean daily values of 110–120%. Levels steadily decreased in late July and August and were in the 95–100% range by early September and into autumn and winter (USACE, 2002; Johnson *et al*., 2007).

Four aspects of *O. mykiss* depth use were considered, including (1) patterns of median migration depth, (2) differences in median depth during spill and no-spill conditions to test whether fish actively avoided supersaturated conditions, (3) the total proportion of time *O. mykiss* spent at depths expected to provide hydrostatic compensation and (4) the duration of episodes spent in shallow (<2 and <1 m) water. Episode duration in shallow water was used because *O. mykiss* frequently moved up and down in the water column, potentially increasing gas exposure duration, which is a good predictor of GBD expression. Fish migrating deeper than 1 and 2 m would experience hydrostatic compensation of *c*. 10 and 20%, respectively. These compensation levels should have prevented tissue bubble formation given in river TDGS concentrations.

Transmitters were recovered for 302 (74%) of 410 *O. mykiss* and 285 had data suitable for analysis. Of the recovered transmitters, 184 (61%) were collected at Lower Granite Dam, 69 (23%) were returned from the main stem Columbia or Snake Rivers and 49 (16%) were returned from tributaries. There was a potential for GBD or other gas supersaturated related mortality to bias the sample because the RDSTs had to be recovered. Any fish that died as a result of TDG exposure would have been lost from the sample. Analysis of telemetry records throughout the basin, however, indicated that of the 108 unrecovered transmitters, 34% ($n = 37$) were last detected either upstream of Priest Rapids Dam (639 rkm) or Lower Granite Dam (695 rkm) where transmitter recovery was unlikely but spawning was likely. To reach these areas, fish had migrated beyond the most supersaturated reaches. Twenty-two per cent ($n = 24$) were last recorded in potential spawning tributaries in the mid or lower Columbia River. A probable maximum mortality related to TDG exposure was therefore *c*. 47 fish (11% of the 410 *O. mykiss* released), though the effect was probably substantially lower. The fish last detected in non-spawning areas were primarily in the main stem Columbia River in areas of active harvest and unreported harvest has been estimated to be 5% in this reach (Caudill *et al*., 2007). Transmitter regurgitation may have accounted for up to an additional 10% (Caudill *et al*., 2007) and other mortality sources (*i.e*. disease, parasites, injury or fallback over dams; Keefer *et al*., 2005) were more likely than GBD. Finally, no evidence of sublethal effects of GBD was observed in fish retrapped at Lower Granite Dam. Consequently, there appeared to be little potential for unrecovered transmitters to substantially bias the sample.

The median *O. mykiss* migration depth was $\geq 2{\cdot}5$ m in all lower Columbia and Snake River reservoirs in both years (Table I). These depths would have provided full hydrostatic compensation at the reported in-river gas levels. Median migration depths were not consistently different between the spill and no-spill conditions in

TABLE I. Medians and 25th and 75th percentiles (in parentheses) for migration depth (m) and consecutive time spent <1 m (s), <2 m (s), >1 m (h) and >2 m (min) (h) >1 m and (min) >2 m by adult *Oncorhynchus mykiss* during migration through the four lower Columbia and three lower Snake River reservoirs

Reservoir	Year	*n*	Median depth (m)	Median consecutive duration of time (s) <1 m	Median consecutive duration of time (s) <2 m	Median consecutive duration of time (h) >1 m	Median consecutive duration of time (min) >2 m
	2000						
BO		112	4·1 (2·9, 6·3)	9·9 (6·2, 20·4)	76·7 (52·9, 94·4)	1·1 (0·2, 5·0)	5·3 (2·5, 27·5)
TD		63	3·9 (3·0, 4·8)	10·8 (7·1, 20·2)	68·5 (56·3, 104·8)	0·5 (0·2, 2·1)	4·2 (2·6, 7·7)
JD		41	3·2 (2·3, 4·2)	17·1 (11·5, 26·7)	105·6 (66·0, 134·0)	0·2 (0·1, 0·4)	3·0 (1·9, 4·9)
MN		30	3·1 (2·4, 4·0)	17·8 (13·1, 23·5)	94·6 (59·3, 126·6)	0·1 (0·1, 0·4)	2·4 (1·4, 5·0)
IH		26	2·9 (2·0, 3·8)	18·9 (13·8, 30·4)	78·1 (60·7, 107·0)	0·1 (0·1, 0·2)	2·0 (1·4, 3·6)
LM		26	2·5 (2·2, 3·3)	23·0 (13·2, 38·9)	88·0 (60·5, 147·3)	0·1 (0·1, 0·3)	2·6 (1·6, 4·4)
GO		24	2·8 (2·1, 3·7)	24·8 (14·0, 31·6)	89·4 (56·3, 112·3)	0·1 (0·1, 0·3)	2·2 (1·4, 5·8)
	2002						
BO		167	4·7 (3·4, 6·4)	12·5 (8·2, 19·2)	79·2 (60·1, 104·1)	1·4 (0·4, 3·5)	7·3 (3·3, 27·9)
TD		118	4·6 (3·5, 5·3)	13·5 (8·9, 21·7)	80·8 (60·5, 126·4)	0·7 (0·2, 1·7)	6·8 (4·1, 10·8)
JD		89	3·7 (2·7, 5·2)	22·0 (12·0, 34·2)	80·0 (59·3, 99·7)	0·1 (0·1, 0·3)	2·4 (1·5, 4·0)
MN		75	3·3 (2·6, 4·4)	28·7 (16·1, 44·9)	95·8 (71·4, 123·0)	0·1 (<0·01, 0·2)	2·9 (2·1, 4·2)
IH		62	2·8 (2·1, 3·5)	23·2 (12·8, 30·9)	69·8 (50·9, 86·9)	0·1 (<0·01, 0·2)	1·7 (1·1, 2·8)
LM		59	2·9 (2·1, 3·6)	21·1 (16·3, 41·4)	78·7 (54·0, 99·3)	0·1 (<0·01, 0·2)	1·8 (1·4, 2·9)
GO		54	2·7 (2·2, 3·5)	26·2 (16·7, 38·1)	79·5 (62·4, 102·3)	0·1 (<0·01, 0·1)	2·0 (1·2, 2·8)

BO, Bonneville; GO, Little Goose; IH, Ice Harbor; JD, John Day; LM, Lower Monumental; MN, McNary; TD, The Dalles.

lower Columbia River reservoirs. In 8 year × reservoir tests, median depths were significantly shallower during spill conditions in two comparisons (Mann–Whitney *U*-test, $P < 0{\cdot}001$), significantly deeper in two comparisons ($P < 0{\cdot}001$), and did not differ ($P > 0{\cdot}05$) in the remaining four cases.

During reservoir migration, *O. mykiss* were at least 2 m below the surface (reducing effective TDG concentrations by at least 20% through hydrostatic pressure compensation) from 64·1% (Ice Harbor) to 83·2% (Bonneville) of the time in 2000 and from 65·2% (Little Goose) to 88·6% (Bonneville) of the time in 2002 (Fig. 1). Fish were deeper than 1 m (providing at least 10% hydrostatic pressure compensation) from 90·4% (Lower Monumental) to 97·7% (The Dalles) of the time in 2000 and 86·5% (Lower Monumental) to 97·1% (The Dalles) of the time in 2002.

Adult *O. mykiss* frequently altered their depth in the water column and typically occupied surface waters in bouts ranging from minutes at a time at depths <2 m to seconds at depths <1 m (Table I). Although near-surface durations were typically short, most *O. mykiss* entered water <1 m deep every few hours (Table I). The median duration >2 m deep in the water column before re-ascending to a depth <2 m was generally several minutes (Table I). Notably, some fish were observed spending several consecutive days at depths shallower than 1 and 2 m (maximum = 22 and 24 days, respectively). These records, however, were almost universally associated with cooler body temperatures, indicating fish were holding in shallow, cold water tributary plumes where dissolved gas levels would be near normally saturated (*i.e.* 100–105% TDGS). This behaviour may be related to thermoregulation and cued by temperature stimuli (High *et al.*, 2006; Keefer *et al.*, 2009) rather than TDGS.

Oncorhynchus mykiss migrating through reservoirs 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 120–130%. The measured TDG concentrations and swimming depths in this study and results from previous studies suggest that *O. mykiss* would have been unlikely to express signs of GBD, especially given the temporal patterns of shallow water use. Past studies suggest that a combination of TDGS, mean swimming depth and the frequency and duration of descents deeper than compensation depth largely determines the development and severity of GBD (Elston *et al.*, 1997; Hans *et al.*, 1999; Weitkamp *et al.*, 2003). Importantly, the time required for emboli formation, the physical appearance of GBD and mortality can vary considerably in response to TDGS level, interindividual GBD susceptibility, emboli location, fish depth, developmental state (juvenile *v.* adult), duration of compensatory depths and other modifying influences (*e.g.* presence of residual bubbles, fish activity and water temperature) (Weitkamp & Katz, 1980; Mesa *et al.*, 2000; Morris *et al.*, 2003). GBD signs become more apparent as duration of exposure at a constant depth increases, though fishes with fluctuating deep and shallow water exposure had fewer signs of GBD and mortality than fishes that were unable to change depths (Knittel *et al.*, 1980; Weitkamp & Katz, 1980). Although *O. mykiss* in this study frequently entered the upper 2 m of the water column, excursions to shallow depths were typically brief and frequent dives below the hydrostatic compensation depth may have allowed gas bubble resorption (Elston *et al.*, 1997; Hans *et al.*, 1999).

It is unknown whether *O. mykiss* can actively detect and avoid supersaturated conditions, either through hydrostatic compensation or movement to areas with lower TDG concentrations. The short periods spent near the surface followed by dives

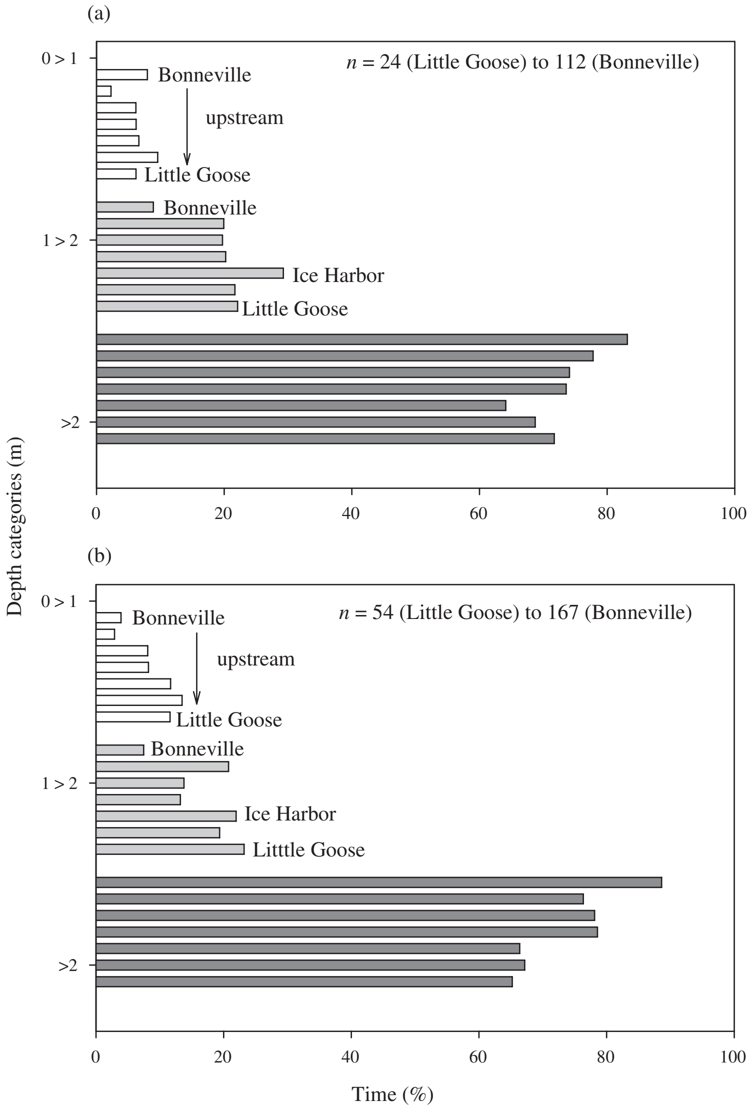

Fig. 1. Percentage of time adult *Oncorhynchus mykiss* tagged with radio data storage transmitters (RDST) spent between the surface and 1, 1–2 and >2 m during migration through the Columbia and Snake Rivers during (a) 2000 and (b) 2002. Bars represent the percentage of time (pooled for all fish) spent at a given depth range.

to deeper water could be interpreted as a response to the physiological effects of supersaturated tissues as they entered pressure conditions near the surface conducive to gas bubble formation. *Oncorhynchus mykiss* tagged in late summer when average TDGS was <105%, however, exhibited nearly identical patterns of frequent and rapid depth changes. From this result, it can be inferred that *O. mykiss* do not have the sensory capabilities to recognize supersaturated water. This result is consistent with observations of *O. tshawytscha* in a concurrent study (Johnson *et al*., 2005,

2007) and suggests that chronic exposure to high TDG concentrations was not a significant component of historic selection regimes.

In both *O. mykiss and O. tshawytscha* telemetry studies, swimming depth appeared to provide adequate hydrostatic compensation. Backman & Evans (2002), however, observed higher GBD prevalence in adult *O. mykiss* than *O. tshawytscha* sampled at Bonneville Dam. Behavioural differences downstream from Bonneville Dam may have contributed to this difference: *O. mykiss* in this study spent *c*. 20% of their total time at depths shallower than 1 m *v*. 1% of the time for *O. tshawytscha* downstream of Bonneville Dam. Other explanations for between-species GBD differences could be related to migration speed, which can be protracted in *O. mykiss*, particularly when water temperatures exceed ~20° C (Keefer *et al*., 2004*b*), or a more general surface orientation in *O. mykiss v. O. tshawytscha*. Tolerance of supersaturated water or differences in migration timing may also play a role (Dawley & Ebel, 1975; Mesa *et al*., 2000).

Overall, these results indicate that *O. mykiss* exhibit complex and variable depth selection behaviour during upstream migration, and that hydrostatic compensation was largely sufficient to prevent expression of GBD. Results reported here are consistent with finer scale observations of dissolved gas exposure histories for individual adult *O. tshawytscha* below Bonneville Dam (Johnson *et al*., 2007). In managed rivers where access to deep water is limited, or in situations where TDGS levels exceed *c*. 130% (*i.e*. high-discharge years in the Columbia River system), hydrostatic compensation may be insufficient to prevent physiological effects from exposure to supersaturated conditions.

Many people provided time and assistance during the course of this study. We thank K. Tolotti, M. Jepson, S. Lee, R. Ringe, C. Boggs, T. Goniea, M. Heinrich, B. High, D. Joosten, M. Morasch, T. Dick and B. Winans at the University of Idaho for helping with field operations and collection and processing telemetry data. A. Matter and B. Burke, National Marine Fisheries Service, helped with data management and analysis. The U.S. Army Corps of Engineers provided funding for this study.

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