REGULATED RIVERS: RESEARCH & MANAGEMENT
Regul. Rivers: Res. Mgmt. **15**: 301–310 (1999)

IDENTIFICATION OF GAS SUPERSATURATION SOURCES IN THE UPPER COLORADO RIVER, USA

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ABSTRACT

Atmospheric gas saturation levels were monitored throughout a 40-km reach of the upper Colorado River during the summer and fall of 1995 to identify possible sources of gas supersaturation in the river. Gas saturation data from seven fixed sampling points and 40 random sampling points were analyzed using analysis of variance (ANOVA) and multiple regression methods. The lowest total gas saturations ($\Delta P = -27$) were found at the bottom release of Williams Fork Reservoir. The highest total gas saturations ($\Delta P = 77$) were found at the spillway release of Windy Gap Reservoir and the confluence of Willow Creek and the Colorado River. Spacial and temporal effects were determined to be significant contributors to gas saturation levels. Gas supersaturation in the study area originated from both man-made and natural sources. Water discharged from the spillway of Windy Gap Reservoir was found to be the main source of man-made supersaturation, while photosynthetic activity of aquatic plants was determined to be the natural source of supersaturation in the study area. Copyright © 1999 John Wiley & Sons, Ltd.

KEY WORDS: gas supersaturation; Colorado River; fish physiology; stream regulation

INTRODUCTION

Gas bubble trauma (GBT), also known as gas bubble disease, is an environmentally induced physiological condition that occurs among fish residing in water that is supersaturated with atmospheric gasses. Supersaturation occurs when total gas pressure (TGP) in a body of water exceeds compensation pressure (PCOMP). TGP is defined as the sum of the gas pressures present in water, including water vapor pressure and PCOMP is equal to barometric pressure plus hydrostatic pressure. While barometric pressure changes with regard to elevation and weather patterns, hydrostatic pressure increases with increased water depth (about 76 mmHg/m). Blood and tissue pressures, as well as surface tension also contribute to compensation pressure, but these are minute and rarely measured (Bouck, 1980).

The difference between TGP and PCOMP is referred to as ΔP. GBT should not occur when ΔP is less than zero (water is not saturated), or equal to zero (water is at equilibrium). If ΔP is greater than zero, the water is supersaturated, and signs of GBT may begin to develop.

Supersaturation can arise from a variety of different man-made and natural sources. For supersaturation to occur, water and atmospheric gasses must be forced together under pressure, or the capacity of water to hold gasses in solution must be reduced. Water and gasses are often mixed under pressure in deep plunge pools below dam spillways or waterfalls when gasses are entrained in falling water. The Columbia River System has a long history of gas supersaturation problems related to the numerous hydroelectric dams present in the drainage (Ebel, 1969; Beiningen and Ebel, 1970). In hatchery systems, water and gas can be mixed unintentionally under pressure when air is drawn into water supplies through leaky pipes (Marsh and Gorham, 1905; Harvey and Smith, 1961). Warm water has a lower capacity to hold dissolved gasses in solution than cold water, and thus, warming of saturated water without a corresponding loss of gas can also result in supersaturation. This is often the case when two saturated bodies of water with different temperatures mix (Adair and Hains, 1974). Loss of hydrostatic pressure

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CCC 0886–9375/99/040301–11$17.50

Received 7 January 1997
Revised 17 April 1998
Accepted 24 August 1998

also reduces the ability of water to hold gasses in solution. This occurs when water is released from deep bottom releases of dams, or escapes from aquifers via wells or springs (Matsue *et al*., 1953). Photosynthetic activity has also been reported to cause supersaturation when the production of oxygen from aquatic plants or algae exceeds the amount of oxygen escaping from the water into the atmosphere (Woodbury, 1941; Boyd *et al*., 1994).

The United States Environmental Protection Agency (1977) suggests 110% saturation (ΔP of 76 mmHg at sea level) as a safe upper limit of supersaturation for freshwater and marine aquatic life. This criterion has been criticized by some researchers for being too high to protect fish from GBT in hatcheries or other situations where fish are restricted to shallow water (Ebel *et al*., 1979; Bouck, 1980). Arguments have also been made that the EPA criterion is too restrictive in natural systems, because fish have been known to avoid supersaturated water (Stevens *et al*., 1980), and fish with access to deep water can sound to increase hydrostatic pressure and avoid developing GBT.

In late August 1994, young-of-the-year rainbow (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) were sampled by Colorado Division of Wildlife personnel from three locations in the Upper Colorado River as part of an ongoing investigation into the disappearance of young-of-the-year rainbow trout in the drainage. One of the factors contributing to the disappearance of these trout is thought to be whirling disease, caused by *Myxobolus cerebralis*, a parasitic myxosporidean. *M. cerebralis* destroys the cartilage of juvenile fish, resulting in a wide variety of clinical signs, including cranial deformities, deformed lower jaws and opercula, blacktail, spinal deformities, disintegration of the fins, opercular cysts, and "whirling" behavior (Halliday, 1976). In addition to typical signs of whirling disease among young-of-the-year trout sampled in 1994, many of the fish exhibited signs of gas bubble trauma. Signs of GBT observed included exophthalmia (protrusion of the eye from its socket) and emboli (bubbles of gas) in the gill lamellae, behind the eye, and in the kidneys. Preliminary sampling at various locations throughout the drainage revealed gas saturation levels ranging from 97.2 to 110.5% ($\Delta P = -16$ to 54 mmHg). Given the severity of GBT signs among the trout sampled and the moderately high TGP readings in the same sampling locations, the present study was initiated to identify sources of supersaturation in the drainage. We hypothesized that gas supersaturation in the drainage varied spatially and temporally. This information was required in order to determine whether or not GBT could be negatively affecting the rainbow trout population.

METHODS

The Colorado River from Granby Reservoir downstream to 5 km west of Parshall, Colorado, was chosen as the study area (Figure 1). This stretch of river has supported viable self-sustaining populations of rainbow and brown trout for over 50 years. Four impoundments occur in the drainage, including Granby Reservoir, Willow Creek Reservoir, Windy Gap Reservoir and Williams Fork Reservoir. Granby Reservoir, Willow Creek Reservoir and Windy Gap Reservoir are all part of the Northern Colorado Water Conservancy District's Windy Gap Project. This series of reservoirs is used to provide water to municipalities on the eastern slope of the Continental Divide in Colorado. Yearly precipitation and demand for water by these municipalities dictates the amount of water released downstream from these reservoirs. A pump station at Windy Gap Reservoir returns water to Granby Reservoir via a 9.6-km long pipeline. No power generating turbines or other mechanisms are used at these reservoirs, and water levels remain fairly constant in the impoundments. At the time the study was initiated, we hypothesized that there was either a point source of supersaturation somewhere in the drainage, or that some seasonal event was causing supersaturation, leading to the GBT signs observed in the young-of-the-year trout in 1994. We designed a sampling protocol providing adequate sample sizes over the course of the field season in order to identify the sources and extent of gas supersaturation in the drainage.

Forty-seven locations were designated throughout the study area to be sampled for gas saturation levels. Seven of these locations were chosen as sampling sites where gas saturation levels would be monitored on a regular basis. These included the outflows of the four reservoirs in the drainage, as well as the confluence of the Colorado River and Willow Creek, the confluence of the Colorado River and the Fraser River, and the confluence of the Colorado River and Williams Fork River. These fixed sampling sites were chosen because they were considered to be possible sources of supersaturation, and were located in fairly widely spaced locations throughout the drainage, allowing good general coverage of the study area. Saturation levels were measured at the outflows directly below each of the dams. Since Windy Gap Reservoir has two separate release locations that operate simultaneously (the spillway release and the fishway release), saturation levels were measured at both locations. Three measurements were taken at each of the three confluences sampled. These included one slightly upstream of the confluence in the tributary arm, one slightly upstream of the confluence in the Colorado River Arm, and one measurement directly in the center of each confluence.

The remaining mainstem of the Colorado River was divided into four 10-km sections (A1–A4), which in turn were each divided into ten 1-km subsections. The subsections were sampled randomly, based on their alphanumeric designation, for gas saturation levels. Twenty-four hour measurements were also made at randomly chosen sampling sites to monitor diurnal fluctuations in TGP.

Gas saturation levels were measured using Common Sensing Inc. Model TBO-L total dissolved gas and oxygen monitors. The monitors measure TGP and oxygen pressure separately, and calculate saturation levels based on water temperature and barometric pressure. Twenty-four-hour measurements were recorded with Common Sensing Inc. DL3 dataloggers attached to Model TBO-L monitors powered by 12-volt batteries. Saturation levels were recorded at each of the seven fixed sampling sites, and four of the remaining 40 random sampling sites (subsections) per sampling day.

Analysis of variance (ANOVA) testing was conducted separately for saturation data collected from the dams and confluences. Because samples were collected at different times of day on each sampling day for each location, we felt that it was appropriate to treat each sample as an individual replicate in this analysis. A two-factor ANOVA was conducted on the dam outflow data to test monthly (June, July, August and September plus October) and location effects on saturation levels. A three-factor ANOVA

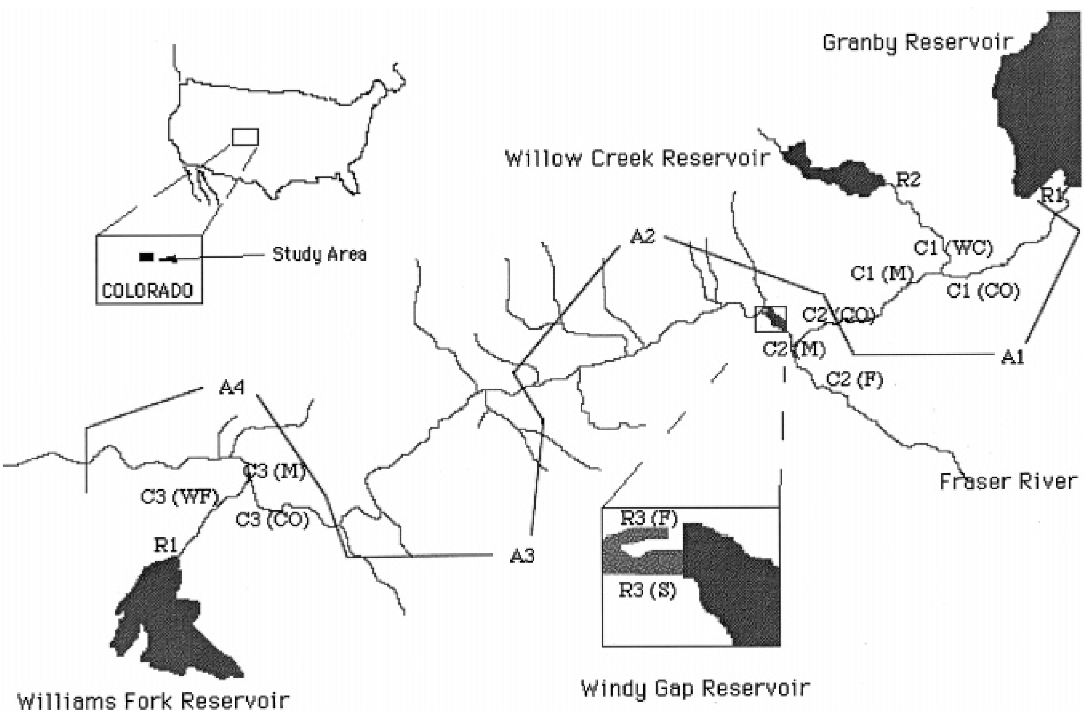

Figure 1. Study area location key for the Upper Colorado River, USA. R denotes reservoir outflows, C denotes locations at tributary confluences and A denotes mainstem river sections

Table I. Location codes and summary statistics for total gas saturation levels (ΔP) at the seven fixed sampling locations and four randomly sampled subsections of the Upper Colorado River from June to October, 1995

Location	Abb.	n	Range
Granby Reservoir outflow	R1	59	−1, 38
Willow Creek Reservoir outflow	R2	56	8, 51
Windy Gap Reservoir spillway	R3 (S)	55	−4, 77
Windy Gap Reservoir fishway	R3 (F)	54	0, 36
Williams Fork Reservoir outflow	R4	56	−27, 43
Willow Creek Confluence (Willow Creek Arm)	C1 (WC)	52	0, 77
Willow Creek Confluence (Colorado Arm)	C1 (CO)	55	0, 40
Willow Creek Confluence (center)	C1 (M)	48	−2, 57
Fraser Confluence (Fraser Arm)	C2 (FR)	54	2, 52
Fraser Confluence (Colorado Arm)	C2 (CO)	55	−7, 47
Fraser Confluence (center)	C2 (M)	53	−3, 45
Williams Fork Confluence (Williams Fork Arm)	C3 (WF)	54	5, 37
Williams Fork Confluence (Colorado Arm)	C3 (CO)	53	2, 40
Williams Fork Confluence (center)	C3 (M)	51	4, 41
First 10 km mainstem Colorado	A1	56	2, 47
Second 10 km mainstem Colorado	A2	56	6, 53
Third 10 km mainstem Colorado	A3	57	0, 42
Fourth 10 km mainstem Colorado	A4	57	4, 42

was conducted on the data from the confluence sampling that tested the effects of confluences, sites within the confluences (arms of the confluences) and month of sampling. Interaction effects of month and sampling location were tested in both ANOVAs for the dam and confluence data.

A multiple regression analysis was conducted on the random subsection samples using month of the year, time of day, and stream kilometer as parameters. As in the ANOVA tests, data from September and October were combined. Time of day was included as a parameter, with most random samples taken from 08:00 to 18:00 h. The stream kilometer parameter was defined as being 1–40, starting at the head of the study area at Granby Reservoir to the bottom of the study area near Parshall, Colorado. A variety of models were created using these factors and interaction effects. Akaiki Information Criterion (AIC) was used to choose the model that best fit the data without over-parameterization. This model was then used to describe the saturation dynamics in the drainage.

RESULTS

Locations of sample sites were assigned alphanumeric codes to simplify location descriptions (Figure 1). Ranges of gas saturation levels for each of the seven fixed sampling locations and each of the four randomly sampled stream sections were summarized (Table I). Mean saturation values and standard deviations by month were summarized for sampling locations (Table II). These results indicate that saturation levels in section A2 were higher than the other sections, and that during June and July, daily saturation levels at two of the regular sampling locations (below Willow Creek Reservoir and below the spillway of Windy Gap Reservoir) were higher than at the other locations.

The highest mean saturation levels among the dams (Table II) were found at the Windy Gap Reservoir spillway during June ($\Delta P = 54.9$) and July ($\Delta P = 62.1$). Saturation levels decreased at this location after the dam stopped spilling in early August, and at that time became comparable with those in the rest of the drainage. Most of the inflow into Windy Gap Reservoir after July was either pumped back up to Granby Reservoir or released through the fishway release. The Willow Creek Reservoir outflow also had high saturation levels in June and July, and the highest mean saturation during the August and September–October sampling ($\Delta P = 22.2$). The Williams Fork Reservoir outflow had mean ΔP values

Table II. Mean total gas saturation values (ΔP) for sampling locations in the Upper Colorado River for June–October, 1995

Location	June		July		August		September–October	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
R1	4.4	5.8	6.2	6.1	13.7	10.9	11.9	7.0
R2	25.7	6.0	35.5	7.8	36.2	11.4	22.2	6.3
R3 (S)	54.9	21.0	62.1	5.4	36.0	23.4	16.2	10.8
R3 (F)	16.4	8.6	18.1	9.3	21.3	9.5	18.7	9.1
R4	10.6	16.7	21.8	18.1	−13.0	11.9	−9.4	10.2
C1 (WC)	19.6	8.8	33.8	22.2	23.7	9.0	24.2	11.2
C1 (CO)	18.2	7.1	16.6	8.5	17.2	6.9	17.0	11.1
C1 (M)	18.9	7.3	31.5	15.2	22.4	8.7	18.4	14.7
C2 (FR)	10.6	5.4	13.2	5.3	19.7	7.7	25.6	13.0
C2 (CO)	18.4	9.1	20.5	13.3	21.3	10.7	24.7	8.0
C2 (M)	16.2	8.2	18.1	10.2	24.0	9.1	23.3	11.4
C3 (WF)	21.6	5.9	14.7	3.4	25.3	8.7	13.0	6.1
C3 (CO)	21.5	7.2	15.4	5.4	25.9	9.9	16.8	7.4
C3 (M)	21.0	3.2	15.7	3.9	28.3	10.4	18.8	5.7
A1	18.4	9.4	22.9	13.7	18.3	8.6	23.2	13.3
A2	36.1	10.2	33.8	12.2	28.3	9.2	20.8	10.3
A3	23.2	6.9	25.2	7.6	20.2	10.7	15.2	9.1
A4	19.9	6.1	14.7	6.8	24.5	10.4	19.5	11.0

below 0 from August to October. These low saturations were presumably owing to stratification of the reservoir, resulting in anoxic conditions at the bottom of the reservoir. Because the outflow of the reservoir is at the base of the dam, low saturation levels were reflected in the outflow measurements. The ANOVA for the dam outflows (Table III) reflect the differences between the dams ($p < 0.0001$) and months ($p < 0.0001$), and verify a month–dam interaction ($p < 0.0001$). The null hypothesis of no temporal or spatial effects on saturation levels was rejected for the dam outflow data.

Differences in saturations were apparent between arms of each of the confluences (Table II). Saturation levels at the Willow Creek Confluence were consistently higher in the Willow Creek Arm and center of the confluence than in the Colorado River Arm. In the Fraser River Confluence, lower saturations were found in the Fraser River Arm than the center of the confluence or the Colorado River Arm in every month except during the September–October sampling period. None of the sites within the Williams Fork Confluence were consistently higher or lower than the other sites throughout the sampling period. The results of the ANOVA for the confluences rejected the null hypothesis of no spatial or temporal effects (Table IV). Significant differences were found between the months of sampling ($p = 0.0175$), between the sites within the confluences ($p = 0.0122$), and a month–confluence interaction was also found ($p = 0.0001$).

The multiple regression model chosen by AIC (Table V) for the mainstem subsection sampling contained the river kilometer, river kilometer squared, time of day and time of day squared as continuous

Table III. ANOVA results for the dam outflow data collected at five outflow sites in the Upper Colorado River during June–October, 1995

Source	df	Type III SS	Mean square	F-value	$p > F$
Dam	4	56119.0366	14029.7592	99.05	0.0001
Month	3	10070.5911	3356.8637	23.70	0.0001
Dam–date	12	21832.0719	1819.3393	12.84	0.0001

Data from September and October were combined for this analysis.

Table IV. ANOVA results for the tributary confluence data collected at three separate confluences and three locations (nested) within each confluence

Source	df	Type III SS	Mean square	F-value	$p>F$
Month	3	1371.3689	457.1229	4.37	0.0175
Confluence	2	439.0625	219.5312	0.55	0.6016
Month–confluence	6	5476.9495	912.8249	8.73	0.0001
Fork (confluence)	6	2380.7134	396.7855	3.80	0.0122
Month–fork (confluence)	18	1882.4959	104.5831	1.17	0.2825

Months included June–October, 1995. Data from September and October were combined for this analysis.

Table V. Gas saturation modeling results for 40 km of the mainstem Upper Colorado River during June–October, 1995

Parameter	df	Estimate	S.E.	Chi square	$p>$Chi square
Intercept	1	−92.7242	12.8789	51.8361	0.0001
River kilometer	1	0.0335	0.2944	0.0129	0.9094
Time of day	1	17.9383	1.9403	85.4707	0.0001
Month	1	−8.9566	3.5916	6.2186	0.0126
River kilometer^2	1	−0.0017	0.0070	0.0587	0.8086
Time of day^2	1	−0.6742	0.0731	85.0967	0.0001
Kilometer–month	1	1.9444	0.4166	21.7875	0.0001
Kilometer^2–month	1	−0.0495	0.0100	24.2935	0.0001
Scale	1	8.8750	0.4202	–	–

variables; June–July and August–October were included as class variables. An interaction between river kilometer and river kilometer squared with the month variables was also included. The second degree polynomials for both river kilometer and time of day reflect the increase in saturation levels in the system up to an inflection point, followed by a subsequent decrease. For example, estimated saturations increased from 08:00 up to 14:00 h, then declined again until 18:00 h (Figures 2 and 3). Saturation levels were similarly affected by river location during June and July. Estimated saturation levels increased as location distance increased up to about stream kilometer 20, where they decreased to the lower end of the sampling area (Figure 2). This spatial change in saturation levels was not as pronounced during August–October,

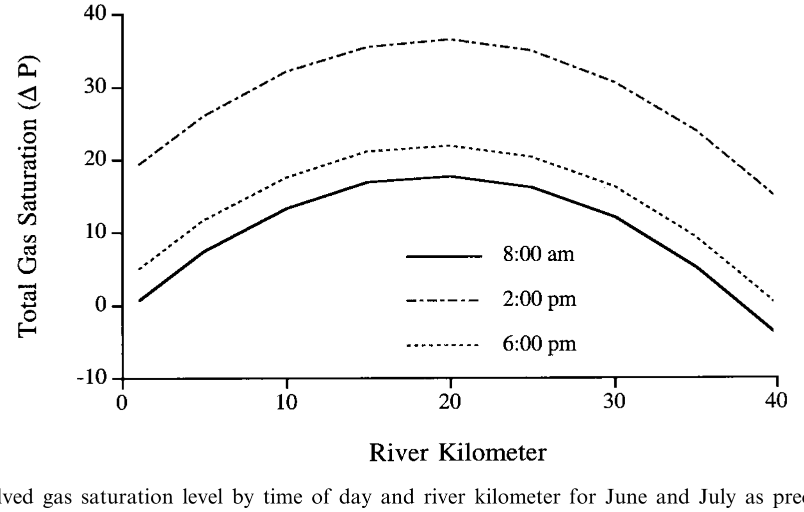

Figure 2. Total dissolved gas saturation level by time of day and river kilometer for June and July as predicted by the multiple regression model

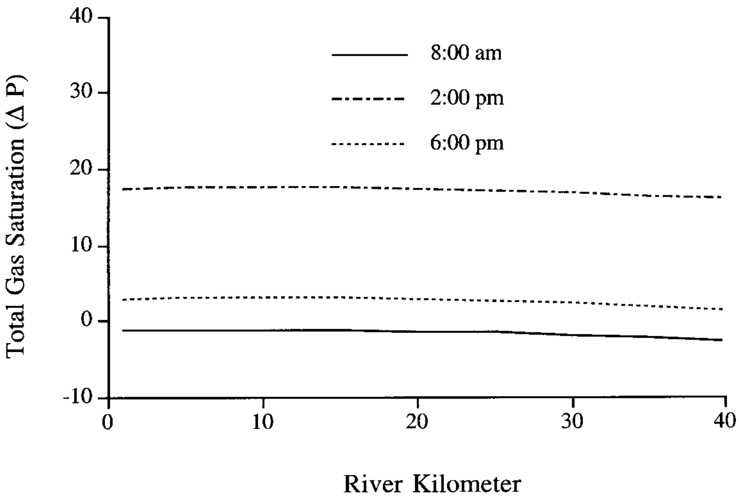

Figure 3. Total dissolved gas saturation level by time of day and river kilometer for June and July as predicted by the multiple regression model

after water stopped flowing over the Windy Gap Reservoir spillway (Figure 3). The model provides a rough overview of the dynamics of the system, and rejects the null hypotheses of no diurnal, temporal or spatial effects on saturation levels in the drainage.

Data from the 24-h sets supported the regression model results of significant diurnal fluctuations in most locations. An example of this diurnal fluctuation (Figure 4) was recorded below Granby Reservoir. While nitrogen saturation values remained relatively stable throughout the 24-h period, oxygen saturation levels increased dramatically during midday, driving up the total gas saturation levels. As with the multiple regression model, the saturation levels increased from 08:00 to 14:00 h and decreased until the end of the day. Total gas saturation did not follow an obvious diurnal fluctuation in some sampling locations. A 24-h measurement at the spillway outflow of Windy Gap Reservoir is an example of this (Figure 5). Total gas saturation in this case was driven by both oxygen and nitrogen supersaturation caused by water falling over the spillway of the dam throughout the entire sampling period. In most other cases where a detectable saturation level of over 100% occurred, the oxygen component, which was driven up by photosynthetic activity, was the cause of supersaturation. In some cases, saturation values actually dropped below 100% at night as respiration exceeded photosynthetic oxygen production (Figure 6).

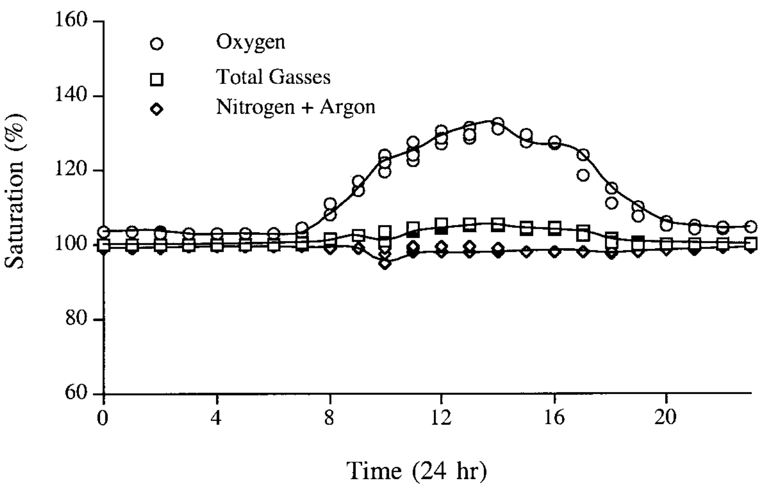

Figure 4. Twenty-four hour measurements of oxygen, nitrogen, and total gas saturation (%) below Granby Reservoir from August 21 to 28, 1995

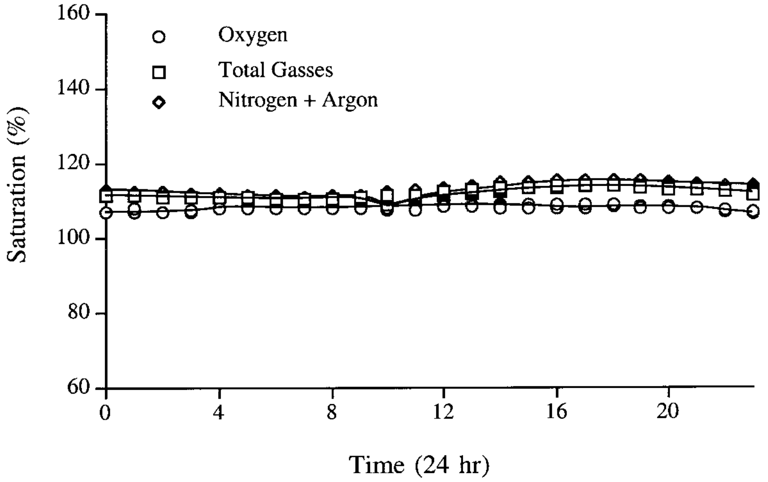

Figure 5. Twenty-four hour measurements of oxygen, nitrogen, and total gas saturation (%) at the spillway of Windy Gap Reservoir from July 28 to 29, 1995

DISCUSSION

The gas saturation levels observed in the drainage were not unusually high for a natural system, especially in the latter months of the study. Bouck (1976) noted that no external symptoms of GBT could be found among wild fish exposed to saturation levels of up to 110%, quite contrary to the occurrence of the disease among fish in raceways at lower saturation levels, and observations by Colorado Division of Wildlife personnel of fingerling rainbow and brown trout with signs of the disease in this drainage.

The results of the gas saturation measurements from fixed sampling points, random sampling points and 24-h sets all indicate that supersaturation in the study area is the result of a combination of natural and man-made causes. Diurnal fluctuations in oxygen saturations were apparent from both random sampling, and 24-h measurements. Heavy mats of *Spirogyra* and other algae were observed throughout much of the study area, and were probably the major contributors to oxygen production. We concluded that the source of natural supersaturation in the sampling area was oxygen production by aquatic plants. The high saturation values at the outflow of Willow Creek Reservoir and the Willow Creek Arm of the

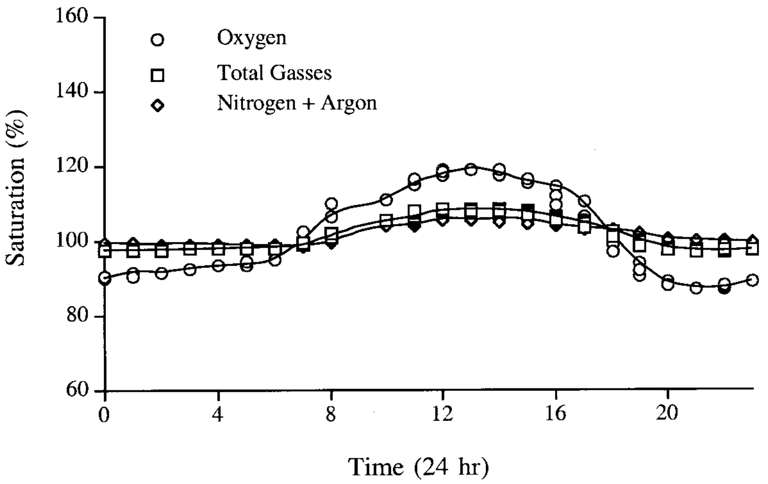

Figure 6. Twenty-four hour measurements of oxygen, nitrogen, and total gas saturation (%) at the center of the Fraser River Confluence from August 31 to September 1, 1995

Colorado River Confluence are most likely a result of the warmer water temperatures and apparent high productivity of that particular tributary. The Fraser River Arm of the Fraser–Colorado River Confluence, however, was typically colder with faster moving water that did not allow much growth of aquatic plants. This was reflected in its lower saturation measurements than those taken at the center of the confluence and the Colorado River Arm of the confluence.

During the latter months of the sampling period, the raw data and the regression model indicated lower saturation levels throughout much of the drainage. The ANOVA results for the dam and confluence data also revealed significant monthly effects on saturation levels. In areas where oxygen was the major contributor to saturation, this was probably owing to shorter day length and a die-off of aquatic plants. Although weather conditions were not recorded, lower saturation values were almost always observed on cloudy days. In future studies where saturation values may be driven by photosynthetic activity, inclusion of this information into a multiple regression model such as that used in this study, may increase fit of the model and explain more of the variability in the data.

The man-made source of supersaturation in the study area was clearly Windy Gap Reservoir. Supersaturation measurements from the spillway outflow were the highest among all the dam outflows measured, and measurements from the fishway were the third highest among the outflows. In addition, both mean monthly saturation values and the regression model of the mainstem Colorado River showed an increase in supersaturation below the reservoir and a gradual decrease further downstream as the supersaturation subsided. Supersaturation at the reservoir was caused by the entrainment of atmospheric gasses in the water falling over the spillway, and to a lesser extent the water released from the fishway outflow. The gradual decrease in supersaturation downstream was most likely to have been caused by loss of gasses to the atmosphere and dilution with increased water volume. Twenty-four hour measurements at Windy Gap Reservoir confirmed that high continuous levels of saturation existed there while water was pouring over the spillway during June, July, and the beginning of August. This was also reflected by significantly lower saturation levels in the multiple regression model for August–October.

Experiments are presently being conducted in a laboratory setting to determine whether GBT can be induced among whirling disease-infected fish at the saturation levels observed in the study area. Changes in discharge levels from Windy Gap Reservoir may be warranted if these experiments establish that higher morbidity and mortality occur among fish exposed to *M. cerebralis* at these saturation levels.

ACKNOWLEDGEMENTS

The cooperating organizations are the United States Geological Survey, the Colorado Division of Wildlife and Colorado State University.

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