The Effects of Dissolved Oxygen on Steelhead Trout, Coho Salmon, and Chinook Salmon Biology and Function by Life Stage

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Introduction

Adequate concentrations of dissolved oxygen in fresh water streams are critical for the survival of salmonids. Fish have evolved very efficient physiological mechanisms for obtaining and using oxygen in the water to oxygenate the blood and meet their metabolic demands (WDOE 2002). However, reduced levels of dissolved oxygen can impact growth and development of different life stages of salmon, including eggs, alevins, and fry, as well as the swimming, feeding and reproductive ability of juveniles and adults. Such impacts can affect fitness and survival by altering embryo incubation periods, decreasing the size of fry, increasing the likelihood of predation, and decreasing feeding activity. Under extreme conditions, low dissolved oxygen concentrations can be lethal to salmonids.

Literature reviewed for this analysis included EPA guidance, other states' standards, reports that compiled and summarized existing scientific information, and numerous laboratory studies. When possible, species-specific requirements were summarized for the following life stages: migrating adults, incubation and emergence, and freshwater rearing and growth. The following information applies to salmonids in general, with specific references to coho, Chinook, steelhead, and other species of salmonids as appropriate.

Adult Migration

Reduced concentrations of dissolved oxygen can negatively affect the swimming performance of migrating salmonids (Bjornn and Reiser 1991). The upstream migration by adult salmonids is typically a stressful endeavor. Sustained swimming over long distances requires high expenditures of energy and therefore requires adequate levels of dissolved oxygen. Migrating adult Chinook salmon in the San Joaquin River exhibited an avoidance response when dissolved oxygen was below 4.2 mg/L, and most Chinook waited to migrate until dissolved oxygen levels were at 5 mg/L or higher (Hallock et al. 1970).

Incubation/Emergence

Low levels of dissolved oxygen can be directly lethal to salmonids, and can also have sublethal effects such as changing the rate of embryological development, the time to hatching, and size of emerging fry (Spence et al. 1996). The embryonic and larval stages of salmonid development are especially susceptible to low dissolved oxygen levels as their ability to extract oxygen is not fully developed and their relative immobility inhibits their ability to migrate to more favorable conditions. The dissolved oxygen requirements for successful incubation of embryos and emergence of fry is tied to intragravel dissolved oxygen levels. Intragravel dissolved oxygen is typically a function of many chemical, physical, and hydrological variables, including: the dissolved oxygen concentration of the overlying stream water, water temperature, substrate size and porosity, biochemical oxygen demand of the intragravel water, sediment oxygen demand, the gradient and velocity of the stream, channel configuration, and depth of water. As a result the dissolved oxygen concentration within the gravels can be depleted causing problems for salmonid embryos and larvae, even when overlying surface water oxygen levels are suitable (USEPA 1986).

Studies note that water column dissolved oxygen concentrations are typically estimated to be reduced by 1-3 mg/L as water is transmitted to redds containing developing eggs and larvae (WDOE 2002). USEPA (1986) concluded that dissolved oxygen levels within the gravels should be considered to be at least 3 mg/L lower than concentrations in the overlying water. ODEQ (1995) expect the loss of an average of 3 mg/L dissolved oxygen from surface water to the gravels.

Incubation mortality
Phillips and Campbell (1961, as cited by Bjornn and Reiser, 1991) concluded that intragravel dissolved oxygen must average 8 mg/L for embryos and alevins to survive well. After reviewing numerous studies Davis (1975) states that a dissolved oxygen concentration of 9.75 mg/L is fully protective of larvae and mature eggs, while at 8 mg/L the average member of the incubating population will exhibit symptoms of oxygen distress, and at 6.5 mg/L a large portion of the incubating eggs may be affected. Bjornn and Reiser (1991) reviewed numerous references and recommend that dissolved oxygen should drop no lower than 5 mg/L, and should be at or near saturation for successful incubation.

In a review of several laboratory studies, ODEQ (1995) concluded that at near optimum (10°C) constant temperatures acute mortality to salmonid embryos occurs at relatively low concentrations of dissolved oxygen, near or below 3 mg/L. Field studies reviewed by ODEQ (1995) demonstrate that embryo survival is low when the dissolved oxygen content in the gravels drops near or below 5 mg/L, and survival is greater at 8 mg/L.

Silver et al. (1963) performed a study with Chinook salmon and steelhead trout, rearing eggs at various constant dissolved oxygen concentrations and water velocities. They found that steelhead embryos held at 9.5°C and Chinook salmon embryos held at 11°C experienced complete mortality at dissolved oxygen concentrations of 1.6 mg/L. Survival of a large percentage of embryos reared at oxygen levels as low as 2.5 mg/L appeared to be possible by reduction of respiration rates and consequent reduction of growth and development rates.

In a field study Cobel (1961) found that the survival of steelhead embryos was correlated to intragravel dissolved oxygen in the redds, with higher survival at higher levels of dissolved oxygen. At 9.25 mg/L survival was 62%, but survival was only 16% at 2.6 mg/L. A laboratory study by Eddy (1971) found that Chinook salmon survival at 10.4 mg/L (13.5 °C) was approximately 67%, however at dissolved oxygen levels of 7.3 mg/L (13.5 °C) survival dropped to 49-57.6%. At temperatures more suitable for Chinook incubation (10.5 °C) Eddy (1971) found the percent survival remained high (over 90%) at dissolved oxygen levels from 11 mg/L to 3.5 mg/L; however, as dissolved oxygen levels decreased, the number of days to hatching increased and the mean dry weight of the fry decreased substantially. WDOE (2002) also points out that the studies above did not consider the act of emerging through the redds, and the metabolic requirements to emerge would be expected to be substantial. Therefore, it is likely that higher oxygen levels may be needed to fully protect hatching and emergence, than to just support hatching alone.

Incubation growth
Embryos can survive when dissolved oxygen is below saturation (and above a critical level), but development typically deviates from normal (Bjornn and Reiser, 1991). Embryos were found to be smaller than normal, and hatching either delayed or premature, when dissolved oxygen was below saturation throughout development (Doudoroff and Warren 1965, as cited by Bjornn and Reiser 1991).

Garside (1966) found the number of days it took for rainbow trout to go from fertilization to hatching increased as dissolved oxygen concentrations and water temperature decreased. In this study, rainbow trout were incubated at temperatures between 2.5 - 17.5°C and dissolved oxygen levels from 2.5 - 11.3 mg/L. At 10°C and 7.5°C the total time for incubation was delayed 6 and 9 days respectively at dissolved oxygen levels of 2.5 mg/L versus embryos incubated at approximately 10.5 mg/L.

Silver et al. (1963) found that hatching of steelhead trout held at 9.5°C was delayed 5 to 8 days at dissolved oxygen concentrations averaging 2.6 mg/L versus embryos reared at 11.2 mg/L. A smaller delay of hatching was observed at oxygen levels of 4.2 and 5.7 mg/L, although none was apparent at 7.9 mg/L. For Chinook salmon held at 11°C, Silver et al. observed that embryos reared at oxygen levels lower than 11 mg/L experienced a delay in hatching, with the most significant delay in those reared at dissolved oxygen levels of 2.5 mg/L (6 to 9 days). The size of both Chinook and steelhead embryos increased with increases in dissolved oxygen up to 11.2 mg/L. External examination of embryos revealed abnormal structural development in Chinook salmon tested at dissolved oxygen concentrations of 1.6 mg/L, and abnormalities in steelhead trout at concentrations of 1.6 and 2.6 mg/L. The survival of Chinook salmon after hatching was only depressed at the 2.5 mg/L level, the lowest level at which hatching occurred, with lower mortalities occurring at higher velocities. Post hatching survival of steelhead trout could not be determined due to numerous confounding factors.

Shumway et al. (1964) conducted a laboratory study to determine the influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. The experiments were conducted at a temperature of 10°C and oxygen levels generally ranging from 2.5 - 11.5 mg/L and flows from 3 to 750 cm/hour. It was concluded that the median time to hatching decreased and size of fry increased as dissolved oxygen levels increased. For example, steelhead trout embryos reared at 2.9 mg/L hatched in approximately 41 days and had a wet weight of 17 mg, while embryos reared at 11.9 mg/L hatched in 36 days and weighed 32.3 mg. The authors found that a reduction of either the oxygen concentration or the water velocity will reduce the size of fry and increase the incubation period, although the affect of various water velocities tested was less than the effect of the different dissolved oxygen concentrations tested.

WDOE (2002) reviewed various references and found that at favorable incubation temperatures a mean oxygen concentration of 10.5 mg/L will result in a 2% reduction in growth. At other oxygen concentrations, growth is reduced as follows: 8% reduction at oxygen levels of 9 mg/L, 10% reduction at 7 mg/L, and a 25% reduction at 6 mg/L.

Incubation avoidance/preference
Alevin showed a strong preference for oxygen concentrations of 8 - 10 mg/L and moved through the gravel medium to these concentrations, avoiding concentrations from 4 - 6 mg/L (WDOE 2002).

Emergence mortality
"The hatching time, size, and growth rate of developing embryos is proportional to the dissolved oxygen concentrations up to 8 mg/L or greater. The ability of fry to survive their natural environment may be related to the size of fry at hatch (ODEQ 1995)." McMahon (1983) recommends dissolved oxygen levels be ≥ 8 mg/L for high survival and emergence of fry. In a review of controlled field and lab studies on emergence, WDOE (2002) states that average intragravel oxygen concentrations of 6 - 6.5 mg/L and lower can cause stress and mortality in developing embryos and alevin. It is also noted that field studies on emergence consistently cite intragravel oxygen concentrations of 8 mg/L or greater as being associated with or necessary for superior health and survival, oxygen concentrations below 6 - 7 mg/L result in a 50% reduction in survival through emergence, and oxygen concentrations below 5 mg/L result in negligible survival. According to various laboratory studies, the threshold for complete mortality of emerging salmonids is noted to occur between 2 - 2.5 mg/L (WDOE, 2002).

After reviewing numerous literature sources, the USEPA (1986) concluded that the embryonic and larval stages of salmonid development will experience no impairment when water column dissolved oxygen concentrations are 11 mg/L. This translates into an intragravel dissolved oxygen concentration of 8 mg/L (USEPA assumes a 3 mg/L loss between the surface water and gravels). Table 1 from the USEPA (1986) lists the water column and intragravel dissolved oxygen concentrations associated with various health effects. These health affects range from no production impairment to acute mortality.

Table 1: Dissolved oxygen concentrations and their effects salmonid embryo and larval stages (USEPA, 1986).

Level of Effect	Water Column DO (mg/L)	Intragravel DO (mg/L)
No Production Impairment	11	8*
Slight Production Impairment	9	6*
Moderate Production Impairment	8	5*
Severe Production Impairment	7	4*
Limit to Avoid Acute Mortality	6	3*

* A 3 mg/L loss is assumed between the water column dissolved oxygen levels and those intragravel.

Freshwater Rearing and Growth

Swimming and activity

Salmonids are strong active swimmers requiring highly oxygenated waters (Spence 1996), and this is true during the rearing period when the fish are feeding, growing, and avoiding predation. Salmonids may be able to survive when dissolved oxygen concentrations are low (<5 mg/L), but growth, food conversion efficiency, and swimming performance will be adversely affected (Bjornn and Reiser 1991). Davis (1975) reviewed numerous studies and reported no impairment to rearing salmonids if dissolved oxygen concentrations averaged 9 mg/L, while at oxygen levels of 6.5 mg/L "the average member of the community will exhibit symptoms of oxygen distress", and at 4 mg/L a large portion of salmonids may be affected. Dahlberg et al. (1968) state that at temperatures near 20°C any considerable decrease in the oxygen concentration below 9 mg/L (the air saturation level) resulted in some reduction of the final swimming speed. They found that between dissolved oxygen concentrations of 7 to 2 mg/L the swimming speed of coho declined markedly with the decrease in dissolved oxygen concentration.

In a laboratory study, Davis et al. (1963) reported that the maximum sustainable swimming speeds of wild juvenile coho salmon were reduced when dissolved oxygen dropped below saturation at water temperatures of 10, 15, and 20°C. Air-saturation values for these dissolved oxygen concentrations were cited as 11.3, 10.2, and 9.2 mg/L respectively. They found that the maximum sustained swimming speeds (based on first and second swimming failures at all temperatures) were reduced by 3.2 - 6.4%, 5.9 - 10.1%, 9.9 - 13.9%, 16.7 - 21.2%, and 26.6 - 33.8% at dissolved oxygen concentrations of 7, 6, 5, 4, and 3 mg/L respectively. The authors also conducted tests on juvenile Chinook salmon and found that the percent reductions from maximum swimming speed at temperatures ranging from 11 to 15°C were greater than those for juvenile coho. At the dissolved oxygen concentrations listed above swimming speeds were decreased by 10%, 14%, 20%, 27%, and 38% respectively.

WDOE (2002) reviewed various data and concluded that swimming fitness of salmonids is maximized when the daily minimum dissolved oxygen levels are above 8 - 9 mg/L. Jones et al. (1971, as cited by USEPA 1986) found the swimming speed of rainbow trout was decreased 30% from maximum at dissolved oxygen concentrations of 5.1 mg/L and 14°C. At oxygen levels of

3.8 mg/L and a temperature of 22°C, they found a 43% reduction in the maximum swimming speed.

Growth

In a review of constant oxygen exposure studies WDOE (2002) concluded salmonid growth rates decreased less than 10% at dissolved oxygen concentrations of 8 mg/L or more, less than 20% at 7 mg/L, and generally less than 22% at 5 - 6 mg/L. Herrmann (1958) found that the mean percentage of weight gain in juvenile coho held at constant dissolved oxygen concentrations was 7.2% around 2 mg/L, 33.6% at 3 mg/L, 55.8% near 4 mg/L, and 67.9% at or near 5 mg/L. In a laboratory study Fischer (1963) found that the growth rates of juvenile coho exposed to constant oxygen concentrations ranging from 2.5 to 35.5 mg/L (fed to satiation, temperature at approximately 18 °C) dramatically decreased with decreases in the oxygen concentration below 9.5 mg/L (air saturation level). WDOE (2002) concludes that a monthly or weekly average concentration of 9 mg/L, and a monthly average of the daily minimum concentrations should be at or above 8 - 8.5 mg/L to have a negligible effect (5% or less) on growth and support healthy growth rates.

Food conversion efficiency is related to dissolved oxygen levels and the process becomes less efficient when oxygen concentrations are below 4 - 4.5 mg/L (ODEQ 1995). Bjornn and Reiser (1991) state that growth, food conversion efficiency, and swimming performance are adversely affected when dissolved oxygen concentrations are <5 mg/L. The USEPA (1986) reviewed growth data from a study conducted by Warren et al. (1973) where tests were conducted at various temperatures to determine the growth of coho and Chinook. USEPA cites that, with the exception of tests conducted at 22 °C, the results supported the idea that the effects of low dissolved oxygen become more severe at higher temperatures.

Brett and Blackburn (1981) performed a laboratory study to determine the growth rate and food conversion efficiency of young coho and sockeye salmon fed full rations. Tests were performed at dissolved oxygen concentrations ranging from 2 to 15 mg/L at a constant temperature of 15°C, the approximate optimum temperature for growth of Pacific Salmon. Both species showed a strong dependence of growth on the environmental oxygen concentrations when levels were below 5 mg/L. For coho, zero growth was observed at dissolved oxygen concentrations of 2.3 mg/L. The mean value for maximum coho growth occurred at 4 mg/L, and at dissolved oxygen concentrations above this level growth did not appear to be dependant on the dissolved oxygen. Sockeye displayed zero growth at oxygen levels of 2.6 mg/L, and reached the zone of independence (growth not dependant on dissolved oxygen levels) at 4.2 mg/L. Brett and Blackburn (1981) conclude that the critical inflection from oxygen dependence to independence occurs at 4 - 4.2 mg/L for coho and sockeye.

Herrmann et al. (1962) studied the influence of various oxygen concentrations on the growth of age 0 coho salmon held at 20 °C. Coho were held in containers at a constant mean dissolved oxygen level ranging from 2.1 - 9.9 mg/L and were fed full rations. The authors concluded that oxygen concentrations below 5 mg/L resulted in a sharp decrease in growth and food consumption. A reduction in the mean oxygen levels from 8.3 mg/L to 6 and 5 mg/L resulted in slight decreases in food consumption and growth. Weight gain in grams per gram of food consumed was slightly depressed at dissolved oxygen concentrations near 4 mg/L, and were markedly reduced at lower concentrations. At oxygen levels of 2.1 and 2.3 mg/L, many fish died and the surviving fish lost weight and consumed very little food.

USEPA (1986) calculated the median percent reduction in growth rate of Chinook and coho salmon fed full rations at various dissolved oxygen concentrations. They calculated no reduction in growth at dissolved oxygen concentrations of 8 and 9 mg/L, and a 1% reduction in growth at 7 mg/L for both species. At 6 mg/L Chinook and coho growth were reduced by 7% and 4% respectively. Dissolved oxygen levels of 4 mg/L result in a 29% reduction in growth for Chinook salmon and 21% reduction in growth for coho. At 3 mg/L there was a 47% decrease in Chinook growth and a 37% reduction in coho growth. USEPA (1986) states that due to the variability inherent in growth studies the reductions in growth rates seen above 6 mg/L are not usually statistically significant, while reductions in growth at dissolved oxygen levels below 4 mg/L are considered severe.

Avoidance and preference

Salmonids have been reported to actively avoid areas with low dissolved oxygen concentrations, which is likely a useful protective mechanism that enhances survival (Davis 1975). Field and laboratory studies have found that avoidance reactions in juvenile salmonids consistently occur at concentrations of 5 mg/L and lower, and there is some indication that avoidance is triggered at concentrations as high as 6 mg/L. Therefore these dissolved oxygen levels should be considered a potential barrier to the movement and habitat selection of salmonids (WDOE 2002).

Spoor (1990) performed a laboratory study on the distribution of fingerling brook trout in dissolved oxygen concentration gradients. Sixteen gradients between 1 and 8.9 mg/L were used for the study to determine what level of dissolved oxygen is preferred by the brook trout. It was found that in the absence of a gradient with dissolved oxygen concentrations at 6 mg/L or more throughout the system, the fish moved freely without showing preference or avoidance. Movement from low to higher oxygen concentrations were noted throughout the study. Fish moved away from water with dissolved oxygen concentrations from 1 - 1.9 mg/L within one hour, moved away from water with dissolved oxygen concentrations of 2 - 2.9 mg/L within 1 - 2 hours, and moved away more slowly from concentrations of 3 - 3.9 mg/L. From his study, Spoor (1996) concluded that brook trout will avoid oxygen concentrations below 4 mg/L, and preferred oxygen levels of 5 mg/L or higher.

Whitmore et al. (1960) performed studies with juvenile coho and Chinook salmon to determine their avoidance reaction to dissolved oxygen concentration of 1.5, 3 , 4.5, and 6 mg/L at variable river water temperatures. Juvenile Chinook salmon showed marked avoidance of oxygen concentrations near 1.5, 3, and 4.5 mg/L in the summer at mean temperatures ranging from 20.7 - 22.8°C, but no avoidance to levels near 6 mg/L at a mean temperature of 18.4°C. Chinook did not show as strong an avoidance to these oxygen levels in the fall when water temperatures were lower, ranging from 11.8 - 13.2°C. Chinook showed little avoidance of dissolved oxygen concentrations near 4.5 mg/L during the fall, and no avoidance to concentrations near 6 mg/L. In all cases avoidance became progressively larger with reductions in the oxygen concentration below 6 mg/L. Seasonal differences of avoidance are most likely due to differences in water temperature. At temperatures ranging from 18.4 - 19°C juvenile coho salmon showed some avoidance to all of the above oxygen concentrations, including 6 mg/L. Their behavior was more erratic than that of Chinook, and their avoidance of concentrations near 4.5 mg/L and lower was not as pronounced at corresponding temperatures. The juvenile coho often started upon entering water with low dissolved oxygen and then darted around until they found their way out of the experimental channel.

USEPA (1986) performed a literature review and cites the effects of various dissolved oxygen concentrations on salmonid life stages other than embryonic and larval (Table 2). These effects range from no impairment at 8 mg/L to acute mortality at dissolved oxygen levels below 3 mg/L.

Table 2: Dissolved oxygen concentrations and their effects on salmonid life stages other than embryonic and larval (USEPA, 1986).

Level of Effect	Water Column DO (mg/L)
No Production Impairment	8
Slight Production Impairment	6
Moderate Production Impairment	5
Severe Production Impairment	4
Limit to Avoid Acute Mortality	3

Lethality

Salmonid mortality begins to occur when dissolved oxygen concentrations are below 3 mg/L for periods longer than 3.5 days (US EPA 1986). A summary of various field study results by WDOE (2002) reports that significant mortality occurs in natural waters when dissolved oxygen concentrations fluctuate the range of 2.5 - 3 mg/L. Long-term (20 - 30 days) constant exposure to mean dissolved oxygen concentrations below 3 - 3.3 mg/L is likely to result in 50% mortality of juvenile salmonids (WDOE, 2002). According to a short-term (1 - 4 hours) exposure study by Burdick et al. (1954, as cited by WDOE, 2002), in warm water (20 - 21°C) salmonids may require daily minimum oxygen levels to remain above 2.6 mg/L to avoid significant (50%) mortality. From these and other types of studies, WDOE (2002) concluded that juvenile salmonid mortality can be avoided if daily minimum dissolved oxygen concentration remain above 3.9 mg/L, and the monthly or weekly average of minimum concentrations remains above 4.6 mg/L.

REFERENCES

Bjornn, T. and D. Reiser. 1991. Habitat requirements of salmonids in streams. In Meehan, W. ed., Influences of Forest and Rangeland Management on Salmonids Fishes and Their Habitat. American Fisheries Society Special Publication 19. pp. 83-138.

Brett, J. R., and J.M. Blackburn. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15C. Can. J. Fish. Aquat. Sci. 38:399-404.

Cobel, D.W. 1961. Influence of water exchange and dissolved oxygen in redds on survival of steelhead trout embryos. Transactions of the American Fisheries Society. 90:469-474.

Dahlberg, M.L., D.L. Shumway, and P. Doudoroff. 1968. Influence of dissolved oxygen and carbon dioxide on swimming performance of largemouth bass and coho salmon. Journal of the Fisheries Research Board of Canada. 25(1):49-70.

Davis, G.E., J. Foster, C.E. Warren, and P. Doudoroff. 1963. The influence of oxygen concentration on the swimming performance of juvenile pacific salmon at various temperatures. Transactions of the American Fisheries Society. 92:111-124.

Davis, J.C. 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on canadian species: a review. Journal of the Fisheries Research Board of Canada. 32:2295-2332.

Eddy, R.M. 1971. The influence of dissolved oxygen concentration and temperature on the survival and growth of Chinook salmon embryos and fry. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 45pp.

Fischer, R.J. 1963. Influence of Oxygen Concentration and of its Diurnal Fluctuations on the Growth of Juvenile Coho Salmon. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 48pp.

Garside, E.T. 1966. Effects of oxygen in relation to temperature on the development of embryos of brook trout and rainbow trout. J. Fish. Res. Bd. Canada 23(8)1121-1134.

Hallock, R.J., R.F. Elwell, and D.H. Fry, Jr. 1970. Migrations of adult king salmon *Oncorhynchus tshawytsca* in the San Joaquin Delta as demonstrated by the use of sonic tags. California Department of Fish and Game, Fish Bulletin 151. 92pp.

Herrmann, R.B. 1958. Growth of juvenile coho salmon at various concentrations of dissolved oxygen. Masters of Science Thesis. Oregon State University. Corvallis, Oregon. 82pp.

Herrmann, R.B., C.E. Warren, and P. Doudoroff. 1962. Influence of oxygen concentration on the growth of juvenile coho salmon. Transactions of the American Fisheries Society. 91:155-167.

McMahon, T.E. 1983. Habitat suitability index models: Coho salmon. U.S. Department of Interior, Fish and Wildlife Service. FWS/OBS-82/10.49. 29pp.

Oregon Department of Environmental Quality (ODEQ). 1995. Dissolved Oxygen: 1992-1994 Water quality standards review. Final Issue Paper. 166pp. Available online at: <http://www.fishlib.org/Bibliographies/waterquality.html>. Website accessed August 20, 2004.

Shumway, D.L., C.E. Warren, and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Transactions of the American Fisheries Society. 93:342-356.

Silver, S.J., C.E. Warren, P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and Chinook salmon embryos at different water velocities. Transactions of the American Fisheries Society. 92(4):327-343.

Spence, B.C., and G.A. Lomnicky, R.M. Hughs, and R.P. Novitzki. 1996. An ecosystem approach to salmonid conversation. TR-4501-96-6057. ManTech Environmental Research Services Corp., Corvallis, Oregon. Available from the National Marine Fisheries Service, Portland, Oregon.

Spoor, W.A. 1990. Distribution of fingerling brook trout, ‚*Salvelinus fontinalis* (Mitchill), in dissolved oxygen concentration gradients. J. Fish. Biol. 36:363-373.

U.S. Environmental Protection Agency (USEPA). 1986. Ambient Water Quality Criteria for Dissolved Oxygen. Office of Water. EPA 440/5-86-003. 35pp. Available online at: <http://www.epa.gov/cgi-bin/claritgw?op-Display&document=clserv:OAR:0579;&rank=4&template=epa>. Website accessed July 5, 2004.

Washington State Department of Ecology (WDOE). 2002. Evaluating Criteria for the Protection of Freshwater Aquatic Life in Washington's Surface Water Quality Standards: Dissolved Oxygen. Draft Discussion Paper and Literature Summary. Publication Number 00-10-071. 90pp.

Whitmore, C.M., C.E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrarchid fishes to low oxygen concentrations. Transactions of the American Fisheries Society. 89:17-26.