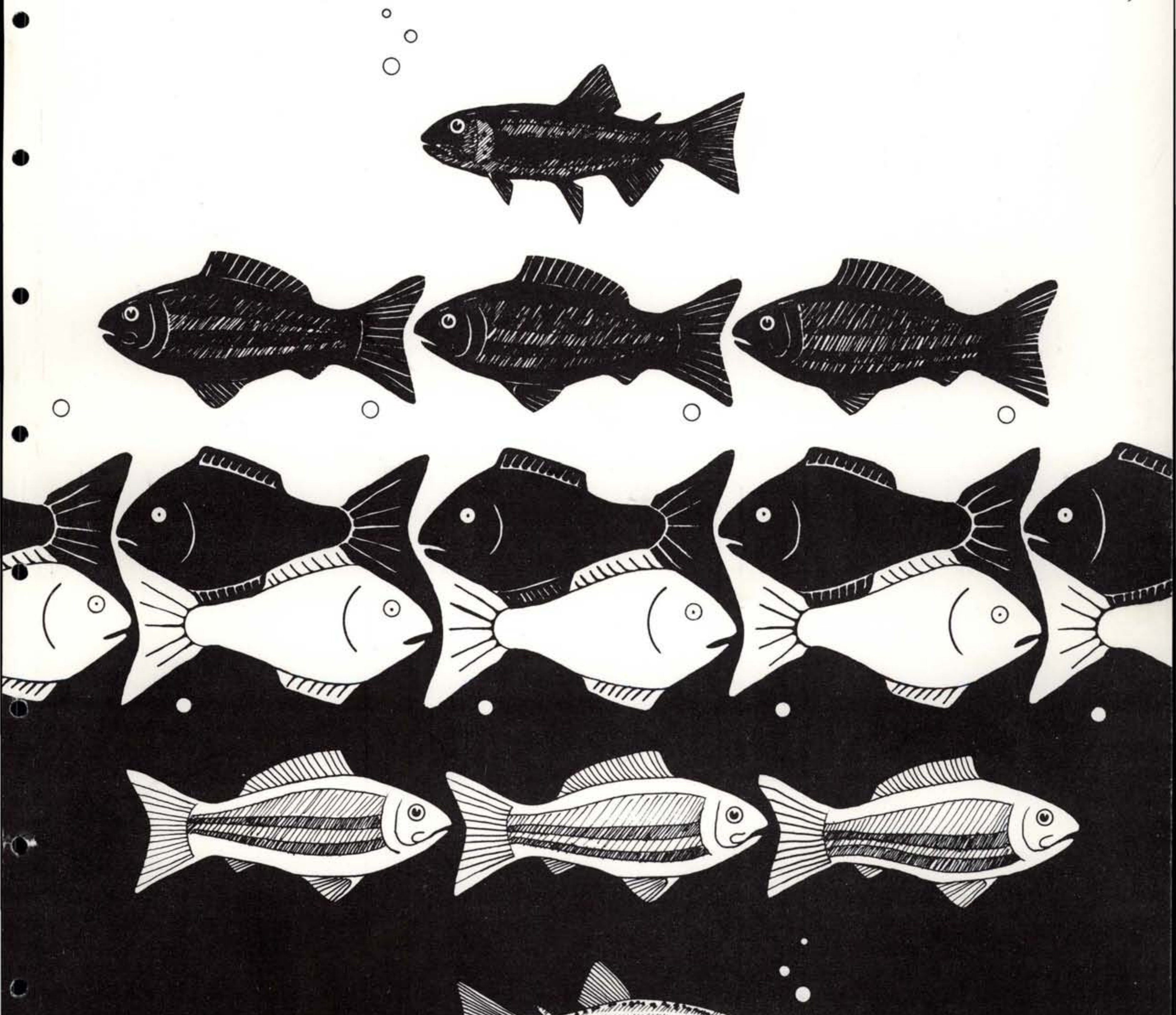
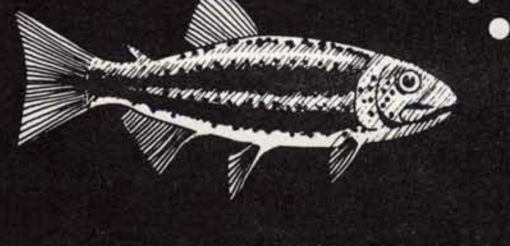
Aquaculture Techniques: Oxygen (pO_2) Requirement For Trout





IDAHO WATER RESOURCE
RESEARCH INSTITUTE

FOREST, WILDLIFE AND RANGE
EXPERIMENT STATION

Research Technical Completion Report
Project A-069-IDA

AQUACULTURE TECHNIQUES:

OXYGEN (pO_2) REQUIREMENT FOR TROUT

QUALITY

by

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and

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Submitted to

Office of Water Research and Technology
United States Department of the Interior
Washington, D.C. 20240

The work on which this report is based was supported in part by funds provided by the United states Department of the interior as authorized under the Water Research and Development Act of 1978.

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February, 1981

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ABSTRACT

Laboratory experiments were conducted to ascertain the partial pressure of oxygen (pO_2) which adversely affected growth of rainbow trout. These experiments, and other data reported previously, indicate that pO_2's greater than 90 mmHg are necessary to maintain allowable growth rates of rainbow trout, and perhaps salmonids, in general.

On the basis of 90 mmHg pO_2, minimum oxygen concentrations (mg/l) for maintenance of allowable growth can be determined. These concentrations delimit the minimum oxygen levels necessary at the outfall of the pond in order to maintain the allowable growth rates of fish. These concentrations will also be very instrumental in determining environmental requirements for instream flows.

The available oxygen, which is the amount of oxygen present for the growth and metabolism of fish in the system, can be calculated using the formula: $AO = DO_{sat} - DO_{90}$ where AO is the available dissolved oxygen (mg/l); DO_{sat} is the mg/l dissolved oxygen in water at a particular elevation and temperature; DO_{90} is the mg/l dissolved oxygen at a partial pressure of 90 mmHg.

INTRODUCTION

A major life limiting constraint in aquatic systems is available dissolved oxygen. Low dissolved oxygen levels have been shown to affect fish species in the following ways: reduce fish growth, decrease feed efficiency, alter feeding behavior, and decrease survival (Davis 1975). Even though these qualitative effects of dissolved oxygen have been documented, the lower limits of dissolved oxygen to avoid these adverse conditions in fish have not been adequately defined. When the minimum oxygen levels necessary to life in aquatic systems are defined, appropriate water quality standards to maintain healthy fish populations can be established more realistically.

Davis (1975) stated "It is my belief that we should look for 'no effect' levels (of dissolved oxygen) in setting water quality criteria to assure the long-term survival of aquatic organisms." Fry (1957) stated: "Any reduction of the oxygen content below the level where the active metabolic rate begins to be restricted is probably unfavorable to the species concerned. From an ecological point of view this 'incipient limiting level' (the critical level at which oxygen becomes a constraint) can be taken as the point where oxygen content becomes unsuitable."

Many investigators have attempted to define the limiting levels of oxygen in the aquatic environment. Ellis et al. (1948) reported that a good mixed fish fauna exists only if the dissolved oxygen concentration is upwards of 5 mg/l. Lietritz and Lewis (1976) stated that the lowest safe level of dissolved oxygen for trout is 5 mg/l but recommended that 7 mg/l dissolved oxygen would be a preferable minimum. Westers and Pratt (1977) and Westers (1979) recommend 5 mg/l as being the minimum dissolved oxygen content of water exiting hatchery ponds. Piper (1972) determined that when oxygen concentrations of water exiting experimental hatchery ponds averaged less than 5 mg/l, growth rates of rainbow trout were reduced. Wedemeyer and Wood (1974) proposed temperature-correlated minimum dissolved oxygen levels for salmon. They believed that increases in water temperature requires higher dissolved oxygen levels to meet the physiological needs of the salmon.

Other researchers have attempted to define oxygen levels using environmental partial pressures of oxygen. Jones et al. (1970), on the basis of data acquired from studies of optimum oxygen transfer across the gill membranes stated that a pO_2 of 118 mmHg was necessary to maintain a proper gradient for oxygen uptake. Randall (1970) calculated that the external-internal dissolved oxygen gradient should be 20 mmHg pO_2. Cameron (1971) reported that rainbow trout blood remains nearly 100% saturated with oxygen until the pO_2 drops below 80 mmHg. Itazawa (1970) reported that rainbow trout blood remains saturated until the environmental pO_2 drops below 100 mmHg. Others have indicated equally as equivocal and seemingly contradictory data (Davis 1975). The reasons for the differences can be attributed to three factors:

1. The investigators were all working with rainbow trout of different sizes, ages and strains.
2. The criteria used in determining the limiting oxygen content differed; some used growth (Piper 1972; Smith 1970; Westers and Pratt 1977), some blood saturations (Cameron 1971; Itazawa 1970), some employed swimming ability (Brett 1962; Jones and Randall 1978) and some used oxygen consumption (Beamish 1964; Klontz et al. 1978).
3. The effects of temperature and elevation on the relationships among dissolved oxygen, oxygen partial pressure, and percent saturation were not taken into account.

This study was designed to consider some of the perceived limitations in determining minimum dissolved oxygen criteria for aquatic environments. We have investigated the physical properties of oxygen in water and the physiological requirements of fish for oxygen in order to determine which standard measure of oxygen, oxygen solubility or oxygen partial pressure, would be most appropriate for setting minimum oxygen levels. In addition, we believe that the determination of the no effect levels of oxygen should include chronic effects of low oxygen, such as reduced growth and altered metabolism. Therefore, we chose trout growth rate as our criterion for determining the adverse affects of low oxygen levels.

This study's objectives were:

1. To explain how oxygen functions in aquatic environments with different water temperatures and at different elevations.
2. To determine which measure(s) of oxygen, solubility ([mg/l] or percent saturation) or partial pressure would be most appropriate for expressing minimum oxygen requirements of aquatic systems.
3. To determine the dissolved oxygen tensions below which the growth rate of rainbow trout is retarded.
4. To demonstrate the practical application of minimum oxygen tension for hatchery practices.

MATERIAL AND METHODS

Water

Moscow City water typically contains 2-3 ppm dissolved oxygen (pO_2 = 40 mmHg). Desired oxygen levels in the experimental systems were maintained by bubbling compressed air into the water and head box of the raceway systems. Additional aeration with pure oxygen was required to saturate system I (control) to > 85% saturation.

Dissolved oxygen content in each system was determined at 8:00 a.m. (minimum of five times per growth period) by Modified Winkler Method (Hach Chemicals Inc.) and maintained at the following levels (Table 1). During the first four growth periods (29 days) dissolved oxygen levels in systems I, II, III, were > 85% saturated (pO_2 = 138.5 mmHg), 50% saturated (pO_2 = 81.5 mmHg), 75% saturated (105.8 mmHg pO_2), respectively. Dissolved oxygen levels during the fifth and six periods (14 days) were maintained at saturations of > 85% saturated (pO_2 = 128 mmHg), 40% saturated (pO_2 = 70.0 mmHg), and 50% saturated (pO_2 = 83.5 mmHg). Dissolved oxygen levels were elevated to > 85%, 68% saturated (pO_2 = 98.0 mmHg), 64% saturated (pO_2 = 93.0 mmHg) during the seventh period (8 days).

The general quality of the dechlorinated Moscow City water used in this study was within acceptable limits for fish culture (Table 2). During the study, however, we discovered that Moscow City water was supersaturated with nitrogen gas (125% saturated). Gas bubble disease, a manifestation of nitrogen gas supersaturation, became increasingly prevalent as the study progressed making continued studies on low oxygen impractical. Gas bubble disease had not been a problem of this lab previously because aeration of the water used to raise oxygen levels also removes nitrogen from the water.

Table 1. Average dissolved oxygen (mg/l) and oxygen partial pressure (mmHg) levels in the three raceway ponds.

Date	Raceway I mmHg-mg/l	Raceway II mmHg-mg/l	Raceway III mmHg-mg/l
5/1-5/7	145 - 9.30	81 - 5.10	113 - 7.13
5/8-5/14	142 - 8.97	79 - 4.97	110 - 6.93
5/15-5/22	138 - 8.46	84 - 5.27	109 - 6.90
5/23-5/29	129 - 8.12	82 - 5.16	89 - 5.64
5/30-6/4	126 - 7.92	68 - 4.31	79 - 4.96
6/5-6/12	130 - 8.23	72 - 4.57	88 - 5.58
6/13-6/20	129 - 8.15	98 - 6.19	93 - 5.83

Table 2. Chemical characteristics of Moscow City water (source: Lai and Klontz 1980).

Parameter	Concentration (mg/l)	Parameter	Concentration (mg/l)
Alkalinity	156.00	Potassium	5.80
Carbon Dioxide	0.00	Sodium	19.60
Total Ammonia	0.03	Iron	0.29
Nitrite	0.008	Manganese	0.07
Nitrate	0.039	Cobalt	< 0.10
Hardness	98.00	Copper	< 0.01
Calcium Hardness	58.00	Zinc	0.05
Magnesium Hardness	40.00	Cadmium	0.04
Calcium	19.70	Silver	< 0.01
Magnesium	10.90		
pH	8.5		

Temperature was measured daily and maintained with chillers at 15 C (+/- 1 C). Water flow in each system was monitored continuously with Signet in-line flow meters (Don-John Inc., Chicago), and maintained at 7 gallons per minute (+/- 0.5 gpm).

Raceway Systems

Three raceway ponds (inside dimensions: 10' long, 1' wide and average depth 0.333 feet; total volume = 3.333 cu ft) (Figure 1) were constructed of plywood coated with fiberglass resin. An inflow of 7 gallons per minute provided a velocity of 0.0526 feet per second and a mean retention time of 3.6 minutes (16.8 changeovers per hour).

Fish

Rainbow trout (*Salmo gaidneri*), averaging 450/pound, were obtained from Spokane Fish Hatchery (Washington Department of Game, Spokane, Washington) on March 27, 1980. The trout were acclimated in the laboratory for one month prior to initiation of the experiments. During the acclimation period, the trout were treated twice with a 1/5000 formalin bath for a clinical outbreak of Gyrodactylus, an external parasitic trematode. Complete examinations were performed on a representative sample of trout prior to the beginning of the experiments. All were found to be free of parasites and overt disease. Trout populations were maintained below .5 lbs/cu ft by removing fish when necessary during pond inventory.

Growth

Growth was measured by wet weight increase, length increase, and net caloric increase during a growth period (1 week). Wet weight increases

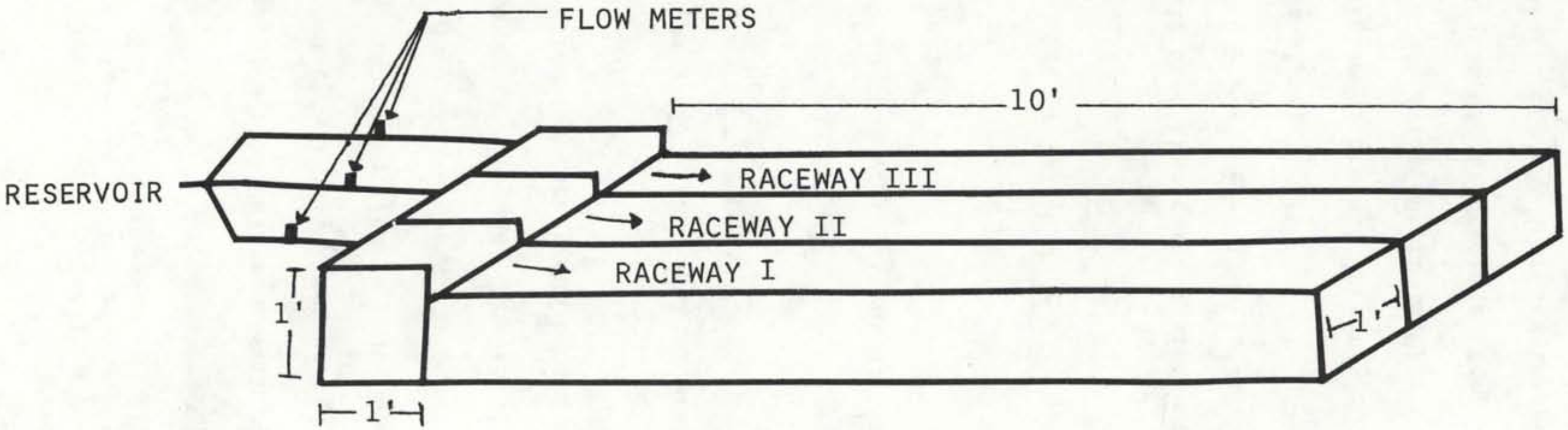


Figure 1. Raceway systems.

were obtained by weighing the total population in a pond with a triple beam balance (+/- 1 gram). The weight increase was expressed as percent weight gain per period.

A random sample (minimum 48 fish) of trout were selected each inventory period and measured (+/- 1 mm). Averages of these length measurements were expressed as percent length gain per period.

Samples of trout from each raceway were collected on May 1, May 15, and May 29, and analyzed by proximate analysis. The total energy content increase during a growth period for each group of trout was determined by the following formula.

$$NC_i = [(WT_i \times \%P_i \times 5.65) + (WT_i \times \%L_i \times 9.4) + (WT_i \times \%NFE \times 4.15)] \quad (1)$$

$$NETC_{inc} = NC_{end} - NC_{beg} \quad (2)$$

where:

NC_i = Net caloric content of the trout at time i (= beginning or end of growth period).

WT_i = Wet weight of trout at time i.

$\%P_i$ = Percent protein of trout at time i, as determined by proximate analysis.

%NFE = Percent nitrogen free extract of trout at time i, as determined

$\%L_i$ = Percent either extract of trout at time i, as determined proximate analysis.

5.65 = 5.65 Kcals/gram of protein (Brett 1980).

9.4 = 9.4 Kcals/gram of fat (Brett 1980).

4.15 = 4.15 Kcals/gram of carbohydrate (Brett 1980).

$NETC_{inc}$ = The net caloric content increase in the trout during the growth period.

Table 3. Proximate analysis and energy content of the 3/64" Oregon Moist Pellet (OMP).

Component	Percent of diet
Protein (crude protein)	38.3
Lipid (ether extract)	11.9
Nitrogen Free Extract	12.3
Fiber	1.5
Ash	10.3
Moisture	25.9
Nitrogen	6.1
Total energy	1256 Kcal/lb*

*Values used in determining caloric content of the diet are (Brett 1980):

Protein	4.23 Kcals/g protein
Lipid	8.00 Kcals/g lipid
Carbohydrate	1.60 Kcals/g carbohydrates

Fish mortalities, which were less than 1% total during the experiment, were weighed and measured, and the size of the fish extrapolated to the end of the growth period. This extrapolated gain was added to the measured gain of the pond.

Nutrition

Oregon Moist Pellet (OMP) (size = 3/64 inch; Moore Clark Inc., LaConner, Washington) was fed throughout the experiment (Table 3). Total food feed daily was determined by Haskell's Feeding Formula (Haskell 1959) with an average hatchery constant of 18.5 (conversion = 1.60,ΔL = .038). Daily ration was fed by hand in four increments, 33.4% at 8:00 a.m. and 22.2% each at 11:00 a.m., 2:00 p.m., 4:00 p.m. Each allotment of food was weighed out individually to the nearest 0.1 grams.

RESULTS AND DISCUSSION

A. Oxygen Partial Pressure; Physical and Physiological Considerations for Meaningful Criteria.

1. Physical Properties of Oxygen in Water.

a. Determination of solubility and partial pressure of oxygen in oxygen saturated water:

The partial pressure of oxygen exerted in an aquatic environment is governed by Dalton's Law. This law states that oxygen gas, which makes up 20.95% of the atmosphere, exerts 20.95% of the total atmospheric pressure. Hutchinson (1957) provides a formula, based on Dalton's Law, to calcualte the oxygen partial pressure (pO_2), when the total atmospheric (or barometric) pressure and water vapor pressure are known. The equation is:

$$pO_2 = 0.2095 \times (P_{atm} - pH_2O) \quad (3) \quad \text{(Hutchinson 1957)}$$

The total average atmospheric pressure for various elevations has been determined (Table 5). Water vapor pressure (pH_2O) which increases as temperature increases have also been measured (Table 4). The effect of elevation on water vapor pressure is so small that it is not considered in pressure calculations.

The partial pressure of oxygen have been calculated for various temperatures and elevations by substituting atmospheric and vapor pressures of Tables 4 and 5 into equation (1), oxygen partial pressures for air saturated water at different temperatures and elevations can be determined (Table 6).

Henry's Law governs the solubility of oxygen in solution. The law stated mathematically is:

$$S_1 = P_1 \quad (4)$$

where:

Table 4. Partial pressure exerted by water vapor (p_{H_2O}) at different temperatures.

Temp. C	Pressure (mmHg)	Temp. C	Pressure (mmHg)
0	4.6	21	18.5
1	4.9	22	19.8
2	5.3	23	20.9
3	5.6	24	22.2
4	6.1	25	23.6
5	6.5	26	25.1
6	7.0	27	26.5
7	7.5	28	28.1
8	8.0	29	29.8
9	8.6	30	31.5
10	9.2	31	33.4
11	9.8	32	38.4
12	10.5	33	37.4
13	11.2	34	39.6
14	11.9	35	41.9
15	12.7	36	44.2
16	13.5	37	46.7
17	14.4	38	49.4
18	15.4	39	52.1
19	16.3	40	55.0
20	17.4	100	760.0

Table 5. Atmospheric pressure for elevations between 0 and 5000 feet above mean sea level (msl).*

Elevation (in feet)	Atmospheric pressure (in mmHg)
0	760.0
1000	731.5
2000	704.0
3000	677.8
4000	653.5
5000	629.3

* Adapted from Cole 1975.

Table 6 . The partial pressure of oxygen (in mmHg) at various temperatures and elevations.

Water temperature °C	Elevation (in feet above msl)					
	0	1000	2000	3000	4000	5000
0	158.26	152.29	146.52	141.04	135.94	130.87
1	158.19	152.22	146.46	140.97	135.88	130.81
2	158.11	152.14	146.38	140.89	135.80	130.73
3	158.05	152.08	146.31	140.83	135.74	130.67
4	157.94	151.97	146.21	140.72	135.63	130.56
5	157.86	151.89	146.13	140.64	135.55	130.48
6	157.75	151.78	146.02	140.53	135.44	130.37
7	157.65	151.68	145.92	140.43	135.34	130.27
8	157.54	151.57	145.81	140.32	135.23	130.16
9	157.42	151.45	145.69	140.20	135.11	130.04
10	157.29	151.32	145.56	140.07	134.98	129.91
11	157.17	151.20	145.43	139.95	134.86	129.79
12	157.02	151.05	145.29	139.80	134.71	129.64
13	156.87	150.90	145.14	139.65	134.46	129.49
14	156.73	150.76	144.99	139.51	134.42	129.35
15	156.56	150.59	144.83	139.34	134.25	129.18
16	156.39	150.42	144.66	139.17	134.08	129.01
17	156.20	150.23	144.47	138.98	133.89	128.82
18	155.99	150.02	144.26	138.77	133.68	128.61
19	155.81	149.83	144.07	138.58	133.49	128.42
20	155.57	149.60	143.84	138.35	133.26	128.19

Calculation of the total oxygen partial pressures (pO_2) for various temperatures.

$$pO_2 = .2095\ (P_{ATM} - P_{H_2O})^*$$

pO_2 = The partial pressure of oxygen at a given temperature and elevation.

.2095 = A constant used to calculate the partial pressure of oxygen present in the total atmosphere pressure. (The atmosphere is 20.95% oxygen.)

P_{ATM} = The atmospheric pressure at a given elevation (Table 2).

P_{H_2O} = The water vapor pressure at a given temperature (Table 1).

*Source; Hutchinson (1957).

S_1 = Solubility of the gas (= oxygen) in liquid (= water).

P_1 = Partial pressure of the gas above the liquid.

It follows that:

$$S_{sea}/P_{sea} = S_{elev}/P_{elev} \qquad (5)$$

or:

$$S_{elev} = (P_{elev}/P_{sea}) \times S_{sea} \qquad (6)$$

where:

S_{elev} = Solubility of oxygen at a particular elevation.

P_{elev} = Partial pressure of oxygen at a particular elevation.

S_{sea} = Solubility of oxygen at sea level.

P_{sea} = Partial pressure of oxygen at sea level.

Oxygen solubility at any temperature and elevation (Table 8) can be calculated by substituting the oxygen partial pressures (Table 6) and solubility values of oxygen for different temperatures at sea level (Table 7) into equation 6.

b. <u>The effects of temperature and elevation on the solubility and partial pressure of oxygen</u>:

Oxygen content in an aquatic environment has been expressed as oxygen solubility (mg/l dissolved oxygen, or percent saturation) or as oxygen partial pressure. As noted previously, these measures are all related (Henry's Law); however, these relationships are not constant. Water temperature and elevation affects oxygen solubility and partial pressure at different rates. The effects of these variables (temperature and elevation) on oxygen solubility and pressure should be considered in order to select suitable minimum oxygen criteria which can be applied to all possible systems (temperatures and elevations).

Table 7. Oxygen solubility of pure water at equilibrium with moist air at sea level.*

Temperature °C	Oxygen (mg/liter)	Temperature °C	Oxygen (mg/liter)
0	14.63	11	11.02
1	14.23	12	10.77
2	13.84	13	10.53
3	13.46	14	10.29
4	13.11	15	10.07
5	12.77	16	9.86
6	12.45	17	9.65
7	12.13	18	9.46
8	11.84	19	9.27
9	11.55	20	9.08
10	11.28		

*Source: Montgomery et al. 1964 (in Cole 1975).

Table 8. Solubility of oxygen in pure water at equilibrium with moist air.

Water temperature °C	0	1000	2000	3000	4000	5000
0	14.63	14.08	13.55	13.04	12.57	12.10
1	14.23	13.69	13.17	12.68	12.22	11.77
2	13.84	13.32	12.81	12.33	11.89	11.44
3	13.46	12.95	12.46	11.99	11.56	11.13
4	13.11	12.61	12.14	11.68	11.26	10.84
5	12.77	12.29	11.82	11.38	10.97	10.55
6	12.45	11.98	11.52	11.09	10.69	10.29
7	12.13	11.67	11.23	10.80	10.41	10.02
8	11.84	11.39	10.96	10.55	10.16	9.78
9	11.55	11.11	10.69	10.29	9.91	9.54
10	11.28	10.85	10.44	10.05	9.68	9.32
11	11.02	10.60	10.20	9.81	9.46	9.10
12	10.77	10.36	9.97	9.59	9.24	8.89
13	10.53	10.13	9.74	9.37	9.03	8.69
14	10.29	9.90	9.52	9.16	8.83	8.49
15	10.07	9.69	9.32	8.96	8.63	8.31
16	9.86	9.48	9.12	8.77	8.45	8.13
17	9.65	9.28	8.93	8.59	8.27	7.96
18	9.46	9.10	8.75	8.42	8.11	7.80
19	9.27	8.91	8.57	8.25	7.94	7.64
20	9.08	8.73	8.40	8.07	7.78	7.48

Calculation of the oxygen solubilities for various temperatures and elevations.

$$DO = DO_{sea} * (pO_{2(elev)} / pO_{2(sea)})$$

DO = The dissolved oxygen content at a given temperature and elevation.

DO_{sea} = The dissolved oxygen content at sea level and at a given temperature (source: Montgomery et al.; Table 3).

$pO_{2(elev)}$ = The partial pressure of oxygen at a given elevation and temperature (Table 4).

$pO_{2(sea)}$ = The partial pressure of oxygen at a given temperature at sea level (Table 4).

Water temperature has a much greater influence on the dissolved oxygen content than on environmental oxygen partial pressure of aquatic systems (Figure 2). Increasing temperature reduces dissolved oxygen content markedly, while oxygen partial pressures are only slightly affected by temperature. For example, dissolved oxygen content of water is reduced by 38% when temperature is increased from 0 to 20°C. The same temperature increase reduces oxygen partial pressure by 2%.

Since a linear relationship exists between the dissolved oxygen content and the oxygen partial pressure exerted at constant temperatures (Henry's Law), decreases in oxygen partial pressures, due to the increases in elevation, results in a proportional decrease of dissolved oxygen content. For example, air saturated water at 5000 feet msl has 17% less dissolved oxygen and 17% less oxygen partial pressure than water with the same temperature at sea level (Table 8). The effects of changes in elevation on the dissolved oxygen content and oxygen partial pressure are the same.

The linear relationship between dissolved oxygen content and oxygen partial pressure also exists in water not saturated with air. At a given temperature and elevation, a 25% reduction in the dissolved oxygen content of the water results in a corresponding 25% decrease in oxygen partial pressure.

To summarize, the solubility of oxygen in aquatic environments is reduced considerably at higher temperatures. A linear relationship exists between the oxygen solubility and oxygen partial pressure in aquatic systems at constant temperatures. Increases in elevation reduce both the oxygen

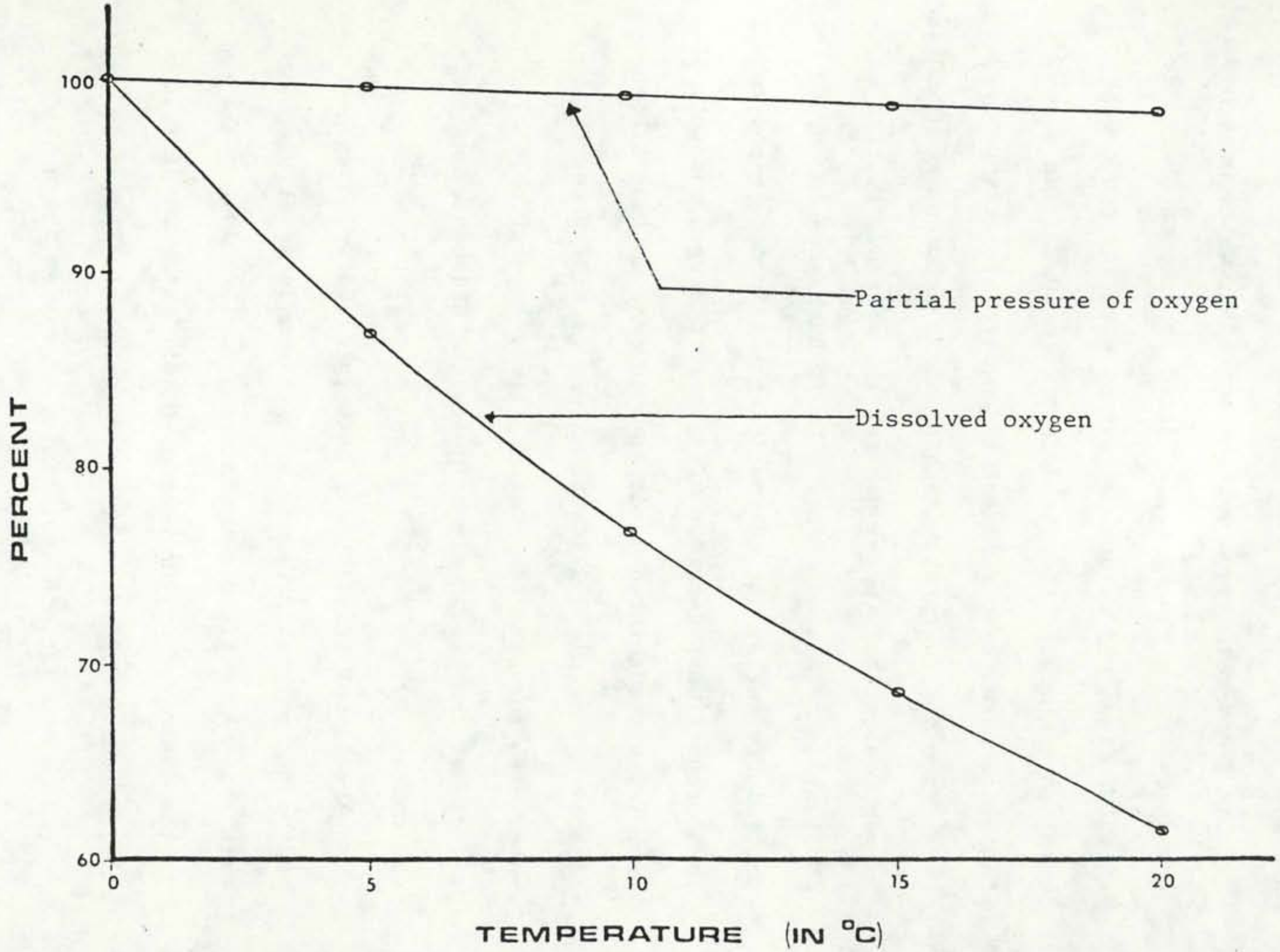


Figure 2. The effect of water temperature on the partial pressure of oxygen and dissolved oxygen.

solubility and partial pressure proportionally. Because of these physical characteristics, pO_2's are more flexible for dealing with various temperatures and elevations.

2. Physiological Requirements of Fish for Oxygen

Lower limits of oxygen for trout have been expressed as dissolved oxygen content (in mg/l) (Piper 1970; Bell 1977; Westers and Pratt 1977), percent saturation (Davis 1975), and as oxygen partial pressure (pO_2) (Cameron 1970; Itazawa 1971). As mentioned previously, these limits are related, but these relationships vary according to water temperature and elevation. Choosing any one of these measures for developing minimum oxygen criteria for aquatic systems should also include the physiological requirements of fish for oxygen.

Oxygen uptake by fish has been shown to be dependent upon the oxygen partial pressure of the water, not the dissolved oxygen content (Graham 1949; Shepard 1955; Davis 1975). Brett (1980) proposed a qualitative model depicting this relationship among oxygen uptake and environmental partial pressures and other variables (partial pressure of oxygen in the blood and the gill lamellar thickness). The model is:

$$\text{oxygen uptake} = (pO_2 \text{ water} - pO_2 \text{ blood})/\text{lamellar thickness} \quad (7)$$

Randall (1978) stated that a gradient of 20 mmHg of oxygen pressure between blood and water is needed in order to maintain optimum oxygen uptake by fish.

Oxygen uptake by fish can be divided into two distinct zones (Figure 3). In the zone of respiratory independence, the oxygen partial pressure is sufficient and the rate of oxygen uptake by fish is independent of the environmental partial pressure. When

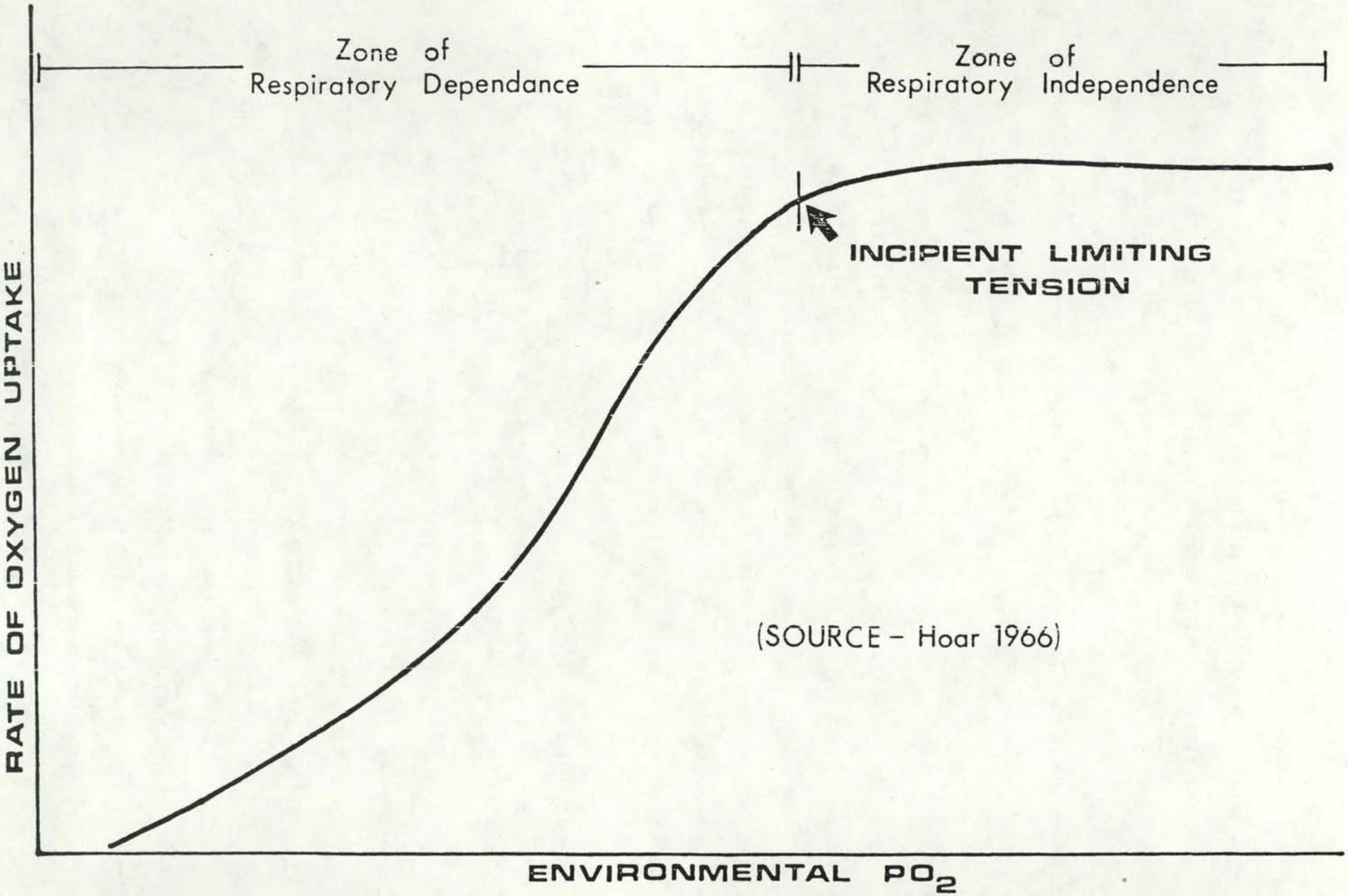


Figure 3. The effect of environmental partial pressure on the rate of oxygen uptake of fish.

environmental pO_2 drops below a critical level, termed the incipient limiting tension, the rate of oxygen uptake by fish is limited and is dependent upon the environmental pO_2. In this zone of respiratory dependence, fish growth and feed conversions can be affected. It is this incipient limiting level which can be considered to be the "no effect" level on growth and metabolism that must be defined in order to establish minimum oxygen levels in aquatic systems.

Davis (1975) developed a strong case for the use of oxygen partial pressures for determining lower oxygen limits in natural aquatic environments. Since there is a strong physiological dependence of fish on oxygen partial pressures, using oxygen partial pressures to determine lower oxygen levels for fish would be practical.

Other researchers (Piper 1970; Westers and Pratt 1977) have proposed the use of constant mg/l dissolved oxygen for minimum oxygen criteria. This constant criteria results in oxygen partial pressures that vary according to temperature (Figure 3). For example, at $0^{o}C$ the environmental pO_2 exerted by 5 mg/l of oxygen is 54.1 mmHg, while the partial pressure of oxygen exerted by 5 mg/l oxygen at 20 C is 85.7 mmHg. This 159% increase is due solely to temperature effects on the dissolved oxygen content of the water. Obviously, 5 mg/l of dissolved oxygen at different temperatures does not provide the same environmental pO_2's and, consequently, life support for fish.

Wedemeyer and Wood (1974) recommended minimum dissolved oxygen levels for salmon which increased with water temperature (Table 9). This increase in minimum dissolved oxygen levels also translates

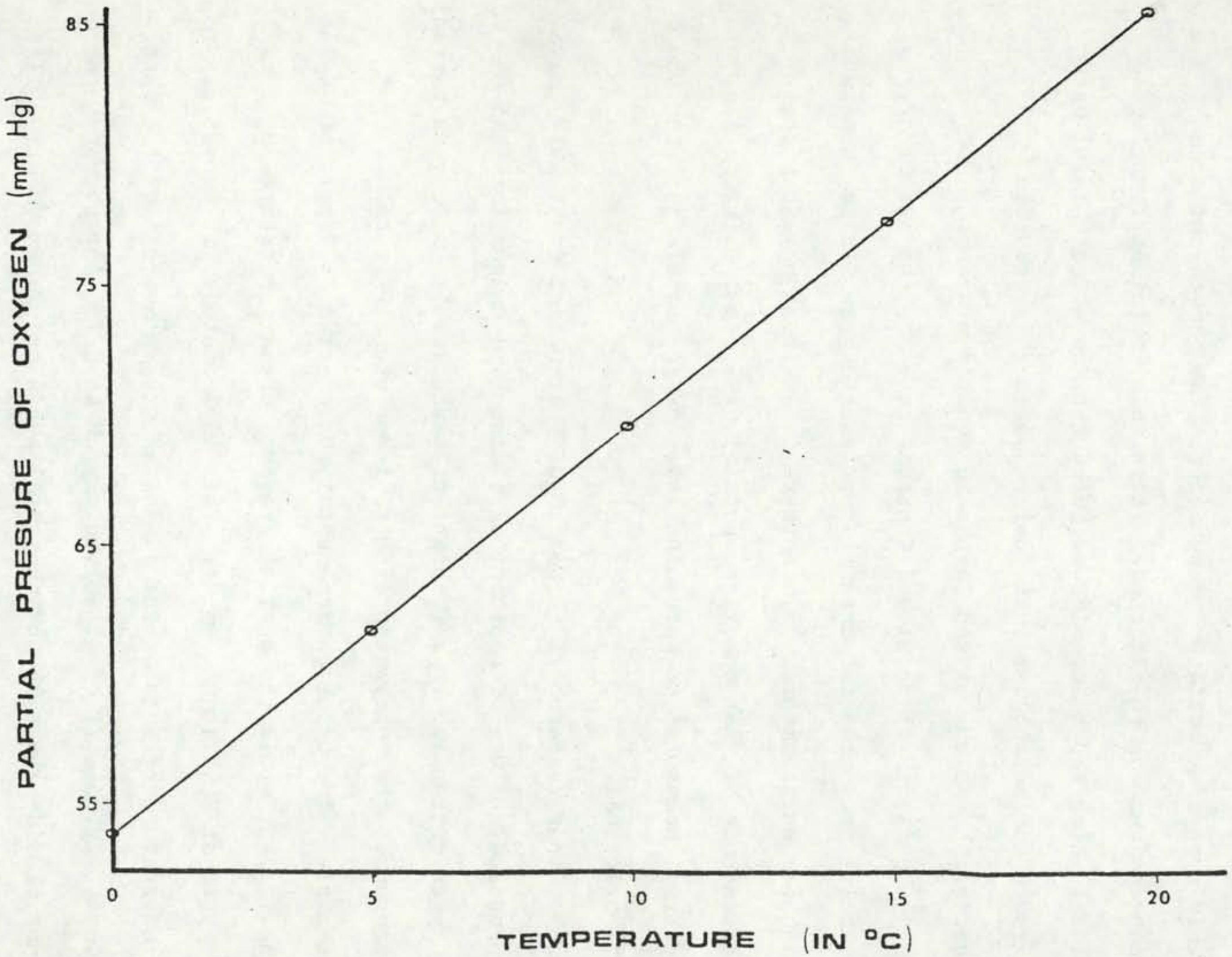


Figure 4. Oxygen partial pressures for 5 mg/l dissolved oxygen at various temperatures.

Table 9. Minimal dissolved oxygen requirements for salmon (modified from Wedemeyer and Wood 1974; in Wedemeyer 1978).

Temperature °C	Dissolved oxygen mg/l	Percent saturation (at sea level)	Partial pressure of oxygen (at sea level)
5	9.1	71.26%	113 mmHg
10	8.8	78.01%	123 mmHg
15	8.3	82.4%	129 mmHg
20	7.8	85.9%	133.7 mmHg

Table 10. Average minimum dissolved oxygen requirements (Level B pO_2 = 90 mmHg) for salmonids expressed as percent saturation (modified from Davis 1975, Table 10).

Temperature °C	Dissolved oxygen mg/l	Percent saturation (at sea level)	Partial pressure of oxygen (at sea level)
0	8.34	57%	90 mmHg
5	7.28	57%	90 mmHg
10	6.43	57%	90 mmHg
15	5.94	59%	92 mmHg
20	5.90	65%	101 mmHg

into different oxygen partial pressure requirements for salmon at different temperatures. At 0 C, the recommended minimum oxygen levels were 7.8 mg/l (113 mmHg pO_2), while at 20 C the recommended level is 10 mg/l (137.5 mmHg pO_2). The authors apparently did not consider the effects of elevation on oxygen requirements of salmon.

Davis (1975) recommended expressing lower limits of oxygen levels depending upon oxygen partial pressure (pO_2 low = 90 mmHg) (Table 10). Percent saturation determined by oxygen partial pressure at saturation or as percent of dissolved oxygen can be calculated by:

$$\% \text{ saturation} = (pO_2 \text{ low}/pO_2 \text{ sat}) \times 100 \quad (8)$$

and: $$\% \text{ saturation} = (DO_{low}/DO_{sat}) \times 100 \quad (9)$$

where:

pO_2 low = the lower limit oxygen partial pressure

pO_2 sat = the oxygen partial pressure of air saturated water

DO_{low} = the lower limit of dissolved oxygen content

DO_{sat} = the dissolved oxygen content of air saturated water (at a given temperature and elevation).

Although temperature effects on oxygen were considered by Davis in getting minimum oxygen criteria, elevation effects are not. For example, at sea level and water temperature of 5 C 54% saturated water exerts a partial pressure of 90 mmHg. However, at same temperature and elevation of 5000 feet msl, 54% saturation of water exerts 70.5 mmHg pO_2. This measure of minimum percent saturation, like that of constant dissolved oxygen levels, does not provide the same life support for fish under all conditions.

Since the rate of oxygen uptake by fish is dependent upon the partial pressure in the environment, we propose using environmental partial pressures rather than oxygen solubility (mg/l dissolved oxygen or percent saturation) for setting minimum oxygen limits for aquatic systems of different temperatures and elevations. Proposing minimum oxygen requirements might seem unreasonable since oxygen is typically measured, either by chemical analysis or oxygen meters, as dissolved oxygen content (mg/l). However, since a linear relationship exists between partial pressures and mg/l oxygen content at constant temperatures, minimum oxygen levels in water based on oxygen partial pressures can be expressed as oxygen solubility (in mg/l dissolved oxygen). Fishery biologists, limnologists, and fish culturists would need only to continue current practices of measuring dissolved oxygen content, water temperature, and elevation (or barometric pressure) rather than pO_2 directly.

B. Experimental Data for Minimum Oxygen Tensions

Wet weight gain, expressed as a percent increase in weight, during the first 4 growth periods (May 1-May 29) did not differ significantly in system I (average = 138.5 mmHg pO_2) and system III (average 105.3 mmHg pO_2) with a 98% and 97.7% increase, respectively. Trout reared an average of 81.5 mmHg pO_2 (system II) increase in weight by 89% or 10% less than systems I and III (Table 11). During the 5th and 6th growth periods oxygen partial pressures in system II and system III were reduced to 70 mmHg and 83.5 mmHg, respectively, while system I tensions remained high (average = 128 mmHg pO_2). Growth rates during these two periods for system II and system III were markedly reduced, averaging 66.6% and 86.3% of system I. Oxygen tensions were elevated during the final (7th) growth period to 98 mmHg and 93 mmHg in systems II and III.

Table 11. Percent weight gain of rainbow trout reared in different oxygen partial pressures.

	Average pO_2	DATE 5/1-5/7	5/8-5/14	5/15-5/22	5/23-5/29	5/30-6/5	6/6-6/12	6/15-6/20
System I	134 mmHg	24.8%	20.3%	28.3%	24.6%	18.3%	20.7%	21.5%
System II	81 mmHg	16.7%	18.0%	28.0%	26.3%	12.6%	13.4%	23.6%
System III	97 mmHg	25.2%	19.1%	31.4%	22.0%	15.9%	17.8%	19.1%

Table 12. Percent length gain of rainbow trout reared in different oxygen partial pressures.

	Average pO_2	DATE 5/1-5/7	5/8-5/14	5/15-5/22	5/23-5/29	5/30-6/5	6/6-6/12	6/13-6/20
System I	134 mmHg	6.23%	7.09%	6.22%	5.22%	6.39%	5.46%	5.56%
System II	81 mmHg	5.33%	4.72%	6.59%	8.79%	6.26%	4.51%	8.68%
System III	97 mmHg	6.61%	5.95%	7.69%	4.57%	6.89%	5.66%	4.22%

Growth rate during this period in system III remained low (88.7% of system I), while raceway II increased significantly (109.7% of system I).

Growth, expressed as total length gain, was not correlated with oxygen tensions (Table 12). During the first 4 growth periods (May 1-May 29), trout in the low oxygen tensions of system II grew faster than their counterparts of system I and system III. There was no difference between system I and system III. Trout growth during growth periods 5 and 6 (May 30-June 12) in the low oxygen levels of system II (average = 70 mmHg pO_2) was lower than system I (average = 128.5 mmHg pO_2), while trout in system III (average = 83.5 mmHg pO_2) grew 6% more than those of system I (Table 8). It appears that length increase of trout is not sensitive to changes in oxygen tensions of the environment.

Increases in net energy content also were not correlated with dissolved oxygen levels. Net caloric increase during the first 4 growth periods (May 1-May 29) was highest in system I (3506 Kcal gain), lowest in system III (2970 Kcal gain), and intermediate in system II (3385 Kcal gain) (Table 13). These results were contrary to what was expected. Since system II had the lowest oxygen tensions in the experiment, higher metabolic costs and consequently lower growth rates, were expected (see equation 3 above). It is possible that these observations might be due to sampling error. During each sampling, only 1 fish was selected randomly from each system. The protein composition of fish assayed in each system was comparable (16.3%, 16.1%, and 16.1% for systems I, II, and III, respectively). The ether extract (= fat) composition of system II, however, was 17% higher than the other two systems (Table 6) due to the high fat content of the trout collected on May 15. If this fish sample of system II was

Table 13. Estimated weekly net caloric content gain (in Kcals) by trout in the three systems.

	5/1-5/7	5/8-5/14	5/15-5/22	5/23-5/29	Total gain
System I	993*	1139	812*	562	3506
System II	981*	1366	631*	407	3385
System III	751*	736	799*	684	2970

* Samples of fish for proximate analysis were collected on May 1, May 15, May 29. Caloric content of trout on May 8 and May 23 were estimated by averaging samples of trout collected 1 week before and 1 week after these dates.

$$NC_i = [(WT_i \times P_i \times 5.65) + (WT_i \times L_i \times 9.4) + (WT_i \times \%NFE \times 4.15)]$$

$$NETC_{inc} = NC_{end} - NC_{beg}$$

where: NC_i = Net caloric content of the trout at time i (= beginning or end of growth period).

WT_i = Wet weight of trout at time i.

TP_i = Percent protein of trout at time i, as determined by proximate analysis.

$\%NFE_i$ = Percent carbohydrate of trout at time i, as determined by proximate analysis.

$\%L_i$ = Percent lipid of trout at time i, as determined by proximate analysis.

5.65 = 5.65 Kcals/gram of protein (Brett 1980).

9.4 = 9.40 Kcals/gram of fat (Brett 1980).

4.15 = 4.15 Kcals/gram of carbohydrate (Brett 1980).

$NETC_{inc}$ = Net caloric content increase in the trout during the growth period.

excluded, the fat content of all three systems would be comparable (8.8%, 8.7%, and 8.7% in systems I, II, and III, respectively). Whether these results were due to sample error or actual changes in body composition can only be determined with additional experiments and increased sample size for proximate analysis.

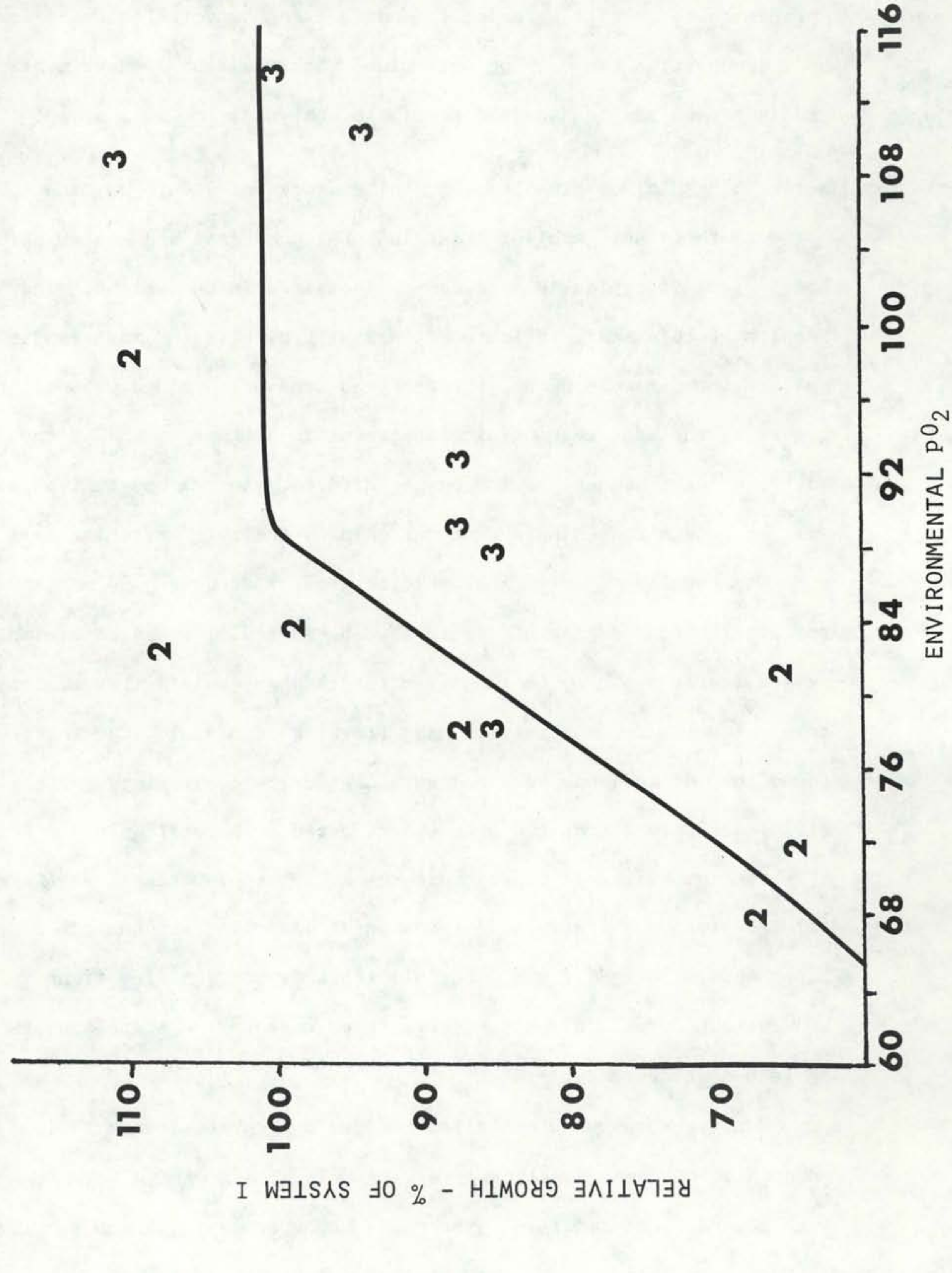
C. Determining Minimum Dissolved Oxygen Tensions for Growth of Trout

Growth (= net gain) of trout in both commercial and conservation hatcheries is typically measured as increases in wet weight. The results of this study indicate wet weight growth is the most sensitive measure for determining no effect oxygen tensions. Since wet weight growth is the most meaningful measurement in hatcheries and is the most sensitive measure of low oxygen effects, minimum oxygen tensions will be determined using wet weight gain as the sole criteria.

The results of wet weight gain of trout reared in $\leq$ 90 mmHg pO_2 results in reduced growth (Figure 5). Davis (1975) averaged minimum oxygen levels reported in the literature and determined that minimum tensions were approximately 90 mmHg (level B in Davis). Cameron (1970) found that 80 mmHg was required to 95% saturate trout blood. Itazawa (1970) determined that 100 mmHg was required to saturate blood. Neither of these investigators considered growth. Other investigators (Piper 1970; Westers and Pratt 1977) recommended dissolved oxygen levels of 5 ppm (pO_2 = 54.1-85.7 mmHg) for all temperatures and elevations. As mentioned previously, there were three reasons why there appears to be such a descrepancy.

Many factors which can alter minimum oxygen requirements of trout have not been considered in this or previous research dealing with lower oxygen limits. Hypertrophy or hyperplasia, which results in increased thickness of the lamellar epithelium of the gill, reduces

Figure 5. Growth rate of rainbow trout (expressed as a percent of system I) in relation to environmental partial pressure. Number points on graph indicate the particular raceway systems' growth at the specific environmental partial pressure



the fish's ability to extract oxygen from the water and thereby requires higher tensions to compensate for this reduced ability. Larmoyeux and Piper (1973) demonstrated an interactive relationship between oxygen and ammonia. High ammonia levels would require oxygen tensions higher than the minimum in order not to impair growth. The effects of carbon dioxide on oxygen transport by blood (Root effect) and on pH-oxygen effect (Bohr effect) also alters minimum oxygen requirements. All of these factors can singly or interactively, alter oxygen requirements of trout. Perhaps future research will incorporate these factors and interactions when determining minimum oxygen levels for trout and other species of fish.

D. Application of Minimum Oxygen Tensions to Fish Culture

Carrying capacity models of hatchery ponds are important tools for managing a hatchery. These models provide a means for the fish culturist and hatchery designer to estimate the total production of fish in a particular hatchery pond. The predictive capabilities of these models depend upon three variables: 1) oxygen consumption by the trout, 2) water flow through the pond, and 3) amount of oxygen available in the water (Table 14).

Oxygen consumption by different sized trout have been determined empirically or indirectly by relating oxygen consumption to feeding rate (see Piper 1970). Many of the existing models have these consumption rates already incorporated.

Available oxygen (AO) for these models have been determined by:

$$AO = DO_{in} - DO_{out} \qquad (10)$$

where:

AO = available oxygen for growth and metabolism (mg/l)

DO_{in} = dissolved oxygen content at the pond infall (mg/l)

DO_{out} = dissolved oxygen content at the outfall of the pond (mg/l).

Table 14. Carrying capacity indexes which require specification of the available oxygen in the water system.

1. Feeding Level Method (Willoughby 1968).

$$\text{Lbs fish/pond} = \frac{(0_{in} - 0_{out}) \times 5.45/100 \times R_w}{\text{Conv} \times \Delta L \times 3 \times L^{-1}}$$

0_{in} = ppm dissolved oxygen in incoming water

0_{out} = ppm dissolved oxygen of water at pond outfall

5.45 = metric tons of water at 1 gpm for 24 hours

100 = grams of oxygen required to metabolize 1200 Kcal

R_w = water inflow in gpm

Conv = feed conversion

ΔL = daily increment of length increase (inches)

3 = weight-length conversion factor

L = length of fish in pond

2. Oxygen Uptake Method (Elliott 1969)

$$\text{Lbs fish/gpm} = \frac{(0_{in} - 0_{out})}{Y_N}$$

0_{in} = ppm dissolved oxygen in incoming water

0_{out} = ppm dissolved oxygen of water at pond outfall

Y_N = oxygen requirement for fish at size 'N'.

3. Oxygen Consumption Method (Liao 1971).

$$\text{Lbs fish/pond} = \frac{1.2\ (0_{in} - 0_{out}) \times R_w}{K \times T^N \times W^m}$$

0_{in} = ppm dissolved oxygen in incoming water

0_{out} = ppm dissolved oxygen of water at pond outfall

1.2 = correction constant

R_w = water inflow in gpm

K = rate constant

T = water temperature in Fehrenheit

N = temperature-water slope

W = weight of individual fish in pounds

m = weight-oxygen slope

Table 15. The dissolved oxygen content (in mg/l) at various temperatures and elevations which exert an oxygen partial pressure of 90 mmHg.*

Water temperature °C	Elevation (in feet above msl) 0	1000	2000	3000	4000	5000
0	8.32	8.32	8.32	8.32	8.32	8.32
1	8.10	8.10	8.10	8.10	8.10	8.10
2	7.88	7.88	7.88	7.88	7.88	7.88
3	7.66	7.66	7.66	7.66	7.66	7.66
4	7.47	7.47	7.47	7.47	7.47	7.47
5	7.28	7.28	7.28	7.28	7.28	7.28
6	7.10	7.10	7.10	7.10	7.10	7.10
7	6.92	6.92	6.92	6.92	6.92	6.92
8	6.76	6.76	6.76	6.76	6.76	6.76
9	6.60	6.60	6.60	6.60	6.60	6.60
10	6.45	6.45	6.45	6.45	6.45	6.45
11	6.31	6.31	6.31	6.31	6.31	6.31
12	6.17	6.17	6.17	6.17	6.17	6.17
13	6.04	6.04	6.04	6.04	6.04	6.04
14	5.91	5.91	5.91	5.91	5.91	5.91
15	5.79	5.79	5.79	5.79	5.79	5.79
16	5.67	5.67	5.67	5.67	5.67	5.67
17	5.56	5.56	5.56	5.56	5.56	5.56
18	5.46	5.46	5.46	5.46	5.46	5.46
19	5.35	5.35	5.35	5.35	5.35	5.35
20	5.25	5.25	5.25	5.25	5.25	5.25

Calculation of dissolved oxygen content that exerts an oxygen partial pressure of 90 mmHg:

$$DO_{(90)} = \frac{90}{pO_{2(sat)}} \times DO_{(sat)}$$

$DO_{(90)}$ = The dissolved oxygen content (in mg/l) which exerts an oxygen partial pressure of 90 mmHg at the given temperature and elevation.

$pO_{2(sat)}$ = The partial pressure of oxygen at saturation for a given temperature and elevation (Table 4).

$DO_{(sat)}$ = The dissolved oxygen content (in mg/l) at saturation for a given temperature and elevation (Table 5).

If the dissolved oxygen is at or near saturation and the dissolved oxygen at the outfall (DO_{out}) is maintained at minimum dissolved oxygen levels, the equation can be written as:

$$AO = DO_{sat} - DO_{min} \qquad (11)$$

where:

AO = available oxygen for growth and metabolism (mg/l)

DO_{sat} = dissolved oxygen content of water at the particular temperature and elevation saturated with oxygen (mg/l)

DO_{min} = minimum dissolved oxygen levels (mg/l).

Generally, minimum dissolved oxygen levels have been assumed to be 5 mg/l, regardless of temperature and elevation. As shown previously, constant dissolved oxygen levels do not provide adequate life support potential for all conditions. Therefore, minimum dissolved oxygen levels (DO_{min}) should be set according to minimum partial pressure, determined to be 90 mmHg. Available oxygen for growth and metabolism can then be computed with these minimum levels with the following formula:

$$DO_{90} = (90/pO_{2\ sat}) \times DO_{sat}) \qquad (12)$$

where:

DO_{90} = the dissolved oxygen content (in mg/l) which exerts an oxygen partial pressure of 90 mmHg at a given temperature and elevation

$pO_{2\ sat}$ = the partial pressure of oxygen in saturated water at the given temperature and elevation (Table 6).

DO_{sat} = the dissolved oxygen content (in mg/l) of saturated water at the given temperature and elevation (Table 8).

90 = the minimum oxygen partial pressure tension (90 mmHg) required for growth and metabolism.

Table 16. Oxygen available (mg/l) for growth and metabolism of fish at different temperatures and elevations.*

Water temperature °C	Elevation (in feet above msl)					
	0	1000	2000	3000	4000	5000
0	6.31	5.76	5.23	4.72	4.25	3.78
1	6.13	5.60	5.08	4.59	4.13	3.67
2	5.96	5.44	4.93	4.45	4.01	3.57
3	5.80	5.29	4.80	4.33	3.90	3.46
4	5.64	5.14	4.67	4.21	3.79	3.37
5	5.49	5.01	4.54	4.10	3.68	3.27
6	5.35	4.88	4.42	3.99	3.59	3.19
7	5.21	4.75	4.30	3.88	3.49	3.10
8	5.08	4.63	4.19	3.78	3.40	3.02
9	4.95	4.51	4.09	3.68	3.31	2.94
10	4.83	4.40	3.98	3.59	3.23	2.86
11	4.71	4.29	3.89	3.50	3.15	2.79
12	4.60	4.19	3.79	3.42	3.07	2.72
13	4.49	4.09	3.70	3.33	2.99	2.65
14	4.38	3.99	3.61	3.25	2.92	2.58
15	4.28	3.90	3.53	3.17	2.85	2.52
16	4.19	3.81	3.45	3.10	2.78	2.46
17	4.09	3.72	3.37	3.03	2.71	2.40
18	4.00	3.64	3.29	2.96	2.65	2.34
19	3.92	3.56	3.22	2.89	2.59	2.29
20	3.83	3.48	3.14	2.82	2.53	2.23

Calculation of available oxygen (AO):

$$AO = D_{sat} - D_{90}$$

D_{sat} = The dissolved oxygen (in mg/l) for 100% saturation at a given temperature and elevation (Table 8).

D_{90} = The dissolved oxygen (in mg/l) that exerts an oxygen partial pressure of 90 mmHg at a given temperature and elevation (Table 15).

These minimum dissolved oxygen values (DO_{90}) (Table 10) can be used in equation 6 to determine available oxygen (Table 11). The equation would be:

$$AO = DO_{sat} - DO_{90} \qquad (11)$$

where:

AO = oxygen available for growth and metabolism (mg/l)

DO_{sat} = the dissolved oxygen content (mg/l) of saturated water at the given temperature and elevation (Table 8)

DO_{90} = the dissolved oxygen content (mg/l) which exerts a oxygen partial pressure of 90 mmHg (Table 15).

These available oxygen (AO) determinations (Table 16) can be substituted into existing models. Prediction of a pond's production by these modified carrying capacity models, would consider both the partial pressure and dissolved oxygen requirements of the trout. The incorporation of both physical criteria, oxygen pressure and content, into existing carrying capacity models enhances predictive capabilities and the flexibility of these models to deal with various temperatures and elevations.

SUMMARY

Oxygen is a major constraint in aquatic systems. Low dissolved oxygen levels reduces fish growth, decreases feed efficiency and survival. Minimum dissolved oxygen levels for salmonids are usually stated as oxygen solubility (mg/l or percent saturation). However, oxygen consumption by fish is not directly dependent upon the oxygen solubility per se, but is dependent upon environmental partial pressure of oxygen.

Oxygen content in an aquatic environment has been expressed as oxygen solubility (mg/l dissolved oxygen and as percent saturation) or as partial pressure. These measures are all related; however, these relationships are not constant. Water temperature and elevation affects oxygen solubility and partial pressure at different rates. Temperature increase of 20°C reduces environmental partial pressure by 2% while dissolved oxygen content is reduced by 38%. At constant temperatures, a linear relationship exists between the dissolved oxygen content and the oxygen partial pressure exerted. Increases in elevation result in proportional decreases in both dissolved oxygen and oxygen partial pressures. Because of these physical characteristics of oxygen, minimum oxygen levels based upon a constant dissolved oxygen content would result in different oxygen partial pressures. Therefore, environmental oxygen partial pressures have been recommended as an appropriate measure for determining minimum oxygen levels in aquatic systems.

Minimum oxygen tensions for growth of trout have been determined to be 90 mmHg. Minimum oxygen levels for trout (in mg/l), based upon this 90 mmHg limit, can be used to determine the available oxygen (corrected for temperature and elevation) for hatchery carrying capacity models. Prediction of a pond's production by these modified models, considers both the oxygen partial pressure and dissolved oxygen requirements of trout. The incorporation

of oxygen partial pressure and oxygen content into existing carrying capacity models enhances predictive capabilities and flexibility of these models to deal with various temperatures and elevations.

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SELECTED WATER RESOURCES ABSTRACT Input Transaction Form	1. *Report No.*	2.	3. *Accession No.*

4. *Title*
Aquaculture Techniques: Oxygen (pO_2) Requirement for Trout Quality

5. *Report Date*
March 1981

6.

8. *Performing Organization Report No.*

7. *Author(s)*
Phil Downey and George W. Klontz

10. *Project No.*
A-069-IDA

9. *Organization*
Idaho Water and Energy Resources Research Institute

11. *Contract/Grant No.*
14-34-0001-0114

12. *Sponsoring Organization*
OWRT

13. *Type of Report and Period Covered.*
Completion

15. *Supplementary Notes*

16. *Abstract*

Laboratory experiments were conducted to ascertain the partial pressure of oxygen (pO_2) which adversely affected growth of rainbow trout. These experiments, and other data reported previously, indicate that pO_2's greater than 80 mmHg are necessary to maintain allowable growth rates of rainbow trout, and perhaps salmonids, in general.

On the basis of 80 mmHg pO_2, minimum oxygen concentrations (mg/1) for maintenance of allowable growth can be determined. These concentration delimit the minimum oxygen levels necessary at the outfall of the pond in order to maintain the allowable growth rates of fish. These concentrations will also be very instrumental in determining environmental requirements for instream flows.

The available oxygen, which is the amount of oxygen present for the growth and metabolism of fish in the system, can be calculated using the formula: $AO = DO_{sat} - DO_{80}$ where AO is the available dissolved oxygen (mg/1); DO_{sat} is the mg/1 dissolved oxygen in water at a particular elevation and temperature; DO80 is the mg/1 dissolved oxygen at a partial pressure of 80 mm Hg.

17a. *Descriptors*
instream flows, salmonids, rainbow trout, oxygen concentrations

17c. *COWRR Field & Group*
08 I

18. *Availability*	19. *Security Class. (Report)*	21. *No. of Pages*	*Send to:*
IWERRI		47	
	20. *Security Class. (Page)*	22. *Price*	

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