

# Influence of Dissolved Oxygen and Carbon Dioxide on Swimming Performance of Largemouth Bass and Coho Salmon<sup>1,2,3</sup>

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## ABSTRACT

The final swimming speed of juvenile largemouth bass, *Micropterus salmoides* (Lacépède), was reduced markedly at oxygen concentrations below 5 or 6 mg/liter in tests at 25 C in a tubular chamber in which the velocity of water was increased gradually, at 10-min intervals, until the fish were forced by the current permanently against a screen. At levels above 6 mg/liter, the final swimming speed was virtually independent of the oxygen concentration. The performance of bass that had been acclimated overnight to elevated carbon dioxide levels was not materially affected by the highest tested concentrations of free carbon dioxide, averaging 48 mg/liter, at any tested level of dissolved oxygen.

For juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), at temperatures near 20 C and carbon dioxide concentrations near 2 mg/liter, any considerable reduction of the oxygen concentration from about 9 mg/liter, the air-saturation level, resulted in some reduction of the final swimming speed. The performance of the salmon was impaired much more markedly than was that of the bass by the same reduction of the oxygen concentration. At oxygen concentrations near and above the air-saturation level, high concentrations of free carbon dioxide averaging 18 and 61 mg/liter had a depressing effect on the final swimming speed of coho salmon even after overnight acclimation. However, this effect decreased at reduced oxygen concentrations. No measurable effect of free carbon dioxide concentrations near 61 mg/liter was evident at 2 mg/liter dissolved oxygen, and concentrations near 18 mg/liter had little or no effect even at moderately reduced dissolved oxygen levels after overnight acclimation of the salmon to these carbon dioxide concentrations.

## INTRODUCTION

THE LITERATURE dealing with the influence of dissolved oxygen on the swimming performance of fishes has been reviewed recently by Doudoroff and Warren (1965), along with much other pertinent literature. Davis et al. (1963) found that even slight reduction of the dissolved oxygen concentration from the air-saturation level usually resulted in some reduction of the maximum sustained swimming speeds of juvenile coho salmon, *Oncorhynchus kisutch*, and chinook salmon, *O. tshawytscha*, at temperatures of 10–20 C. Katz et al.

<sup>1</sup>Received for publication April 10, 1967.

<sup>2</sup>Technical Paper No. 2270, Oregon Agricultural Experiment Station. A contribution from the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University, Corvallis, Oregon.

<sup>3</sup>This investigation was supported in part by U.S. Public Health Service Grant WP-00135.

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(1959) tested the ability of juvenile largemouth bass, *Micropterus salmoides*, 63–93 mm in total length to swim for 1 day against a current at a speed of about 24 cm/sec. In September, at 25 C, the bass were able to resist the current even when the oxygen concentration was only about 2 mg/liter, but in December, at temperatures of 15.5–17 C, they apparently were unable to do so when the oxygen concentration was reduced to 5 mg/liter. The maximum sustained swimming speeds of the bass possible under the various conditions were not determined.

Carbon dioxide has long been known to be toxic to fish (Doudoroff and Katz, 1950) and to reduce the affinity of their blood for oxygen at high as well as reduced oxygen tensions (Root, 1931). Basu (1959) measured the "active" oxygen consumption rates of four species of fish at various concentrations of both dissolved oxygen and carbon dioxide. Steady activity was ensured by mild electrical stimulation whereby the fish were forced to swim in a rotating annular respirometer. Basu found that the logarithm of the oxygen uptake rate declined linearly with increase of carbon dioxide concentration. This decline was much steeper at very low dissolved oxygen levels than at higher levels in the three species tested at the very low levels: the brown bullhead, *Ameiurus nebulosus*; carp, *Cyprinus carpio*; and goldfish, *Carassius auratus*. We know of no comparable experiments on the influence of free carbon dioxide on the swimming speeds of fish at various levels of dissolved oxygen.

The resistance to dissolved oxygen deficiency of resting coho salmon (McNeil, MS, 1956), largemouth bass (Hart, 1945, 1957), and many other species of fish has been found not to be markedly and lastingly reduced at carbon dioxide concentrations below 50 mg/liter. In experiments with coho salmon, the minimum effective carbon dioxide concentrations have been found to vary with the degree of rapidly progressing acclimatization or adjustment of the fish to the elevated carbon dioxide levels (McNeil, MS, 1956). They may also vary somewhat with the bicarbonate alkalinity of the water (McNeil, MS, 1956) and with temperature, but Doudoroff (1957) has pointed out that the wide variation with temperature of effective carbon dioxide *tensions* that has been reported (Fry et al., 1947) does not signify material variation of effective carbon dioxide *concentrations*. Alabaster et al. (1957) found that carbon dioxide concentrations well below 50 mg/liter had a marked effect on the dissolved oxygen requirements of rainbow trout, *Salmo gairdneri*. However, in their tests, the fish evidently were subjected to low oxygen concentrations and high carbon dioxide concentrations suddenly and simultaneously, so that they had no opportunity to become adapted to the elevated carbon dioxide levels before being subjected to critical or lethal dissolved oxygen levels.

The main objective of the present work was evaluation of the influence of carbon dioxide at high, low, and intermediate oxygen concentrations on the maximum sustained swimming speeds of largemouth bass at 25 C and of coho salmon at 20 C. Our initial undertaking, however, was accurate determination,

in late spring and early summer, of the influence of dissolved oxygen on the swimming ability of the bass at 25 C and at a low level of free carbon dioxide.

## MATERIALS AND METHODS

### EXPERIMENTAL FISH

The largemouth bass used in these studies were seined from a pond near Junction City, Oregon. Juvenile coho salmon were seined periodically from tributaries of the Alsea River in Benton County and from the Yaquina River in Lincoln County, Oregon. All fish were graded according to size; the largest and smallest fish were discarded. The mean total length of the bass used was 82 mm; the standard deviation was 2.3 mm. The mean total length of the coho salmon was 82 mm; the standard deviation was 3.9 mm.

The fish were kept in a constant temperature room in 50-gal (189-liter) glass aquaria supplied with running water from a small spring-fed stream. The largemouth bass were held at 25 C, the test temperature, and fed unrestricted rations of small, live earthworms for at least 18 days before use in experiments. Losses of bass in the stock tank were negligible during the experiments. The first lot of coho salmon used was held at 20 C, the test temperature, but heavy losses occurred which were due to an unidentified disease. The use of this lot of fish was discontinued when the disease became apparent and only a small number of the fish had been used. Subsequently, all the coho salmon were held at the lower acclimation temperature of 17 C for at least 5 days before use in experiments, and no more diseased fish were observed. The coho salmon were fed unrestricted rations of tubificid worms during the holding periods.

### EXPERIMENTAL APPARATUS

The experimental apparatus (Fig. 1) was designed for subjecting fish to a rectilinear flow of water of controlled velocity, temperature, and dissolved gas content in a glass tube (test chamber) 1.5 m long and 100 mm in inside diam. It has been described in detail by Davis et al. (1963) and diagrammed by Katz et al. (1959). Filtered stream water, supplied through polyethylene pipe and Tygon tubing, could be circulated continuously, by means of an all-iron centrifugal pump, through the tubular test chamber and through an aluminum heat exchanger immersed in a cooling bath for temperature control. Water velocities in the chamber could be adjusted by means of a gate valve located at the pump's outlet. The valve had an attached graduated dial and an indicator on the handwheel. It was calibrated with a small current meter.

The water in the system was renewed continuously at a rate of 1 liter per minute. Dissolved gas concentrations were maintained by introducing a gas, or gases, at the bottom of a vertical glass column filled with ceramic Raschig rings, through which the water flowed downward before entering the experimental chamber. Nitrogen, compressed air, and oxygen were used for maintaining concentrations of dissolved oxygen below, at, and above air-saturation

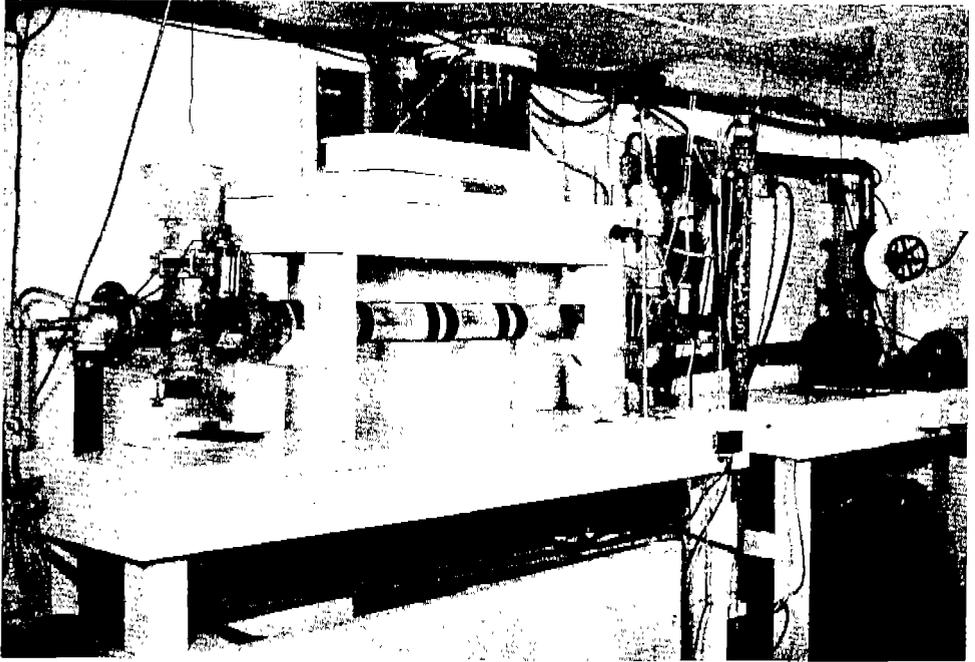


FIG. 1. The experimental apparatus.

levels, respectively. Carbon dioxide was used in combination with the above gases to attain concentrations of this gas above the low level characteristic of the untreated water.

A few minor changes were made in the apparatus described by Davis et al. (1963). A fixed aluminum screen was added behind the movable (retractable) screen at the downstream end of the test chamber, behind the fish-introduction port and funnel. This enabled removal of each fish from the experimental chamber as soon as it was forced by the current against the movable screen, without danger of the fish being swept out of the chamber and through the pump. The control and measurement of the flow of water through the vertical glass column and into the test chamber were facilitated by fitting a ball-displacement flowmeter and a glass stopcock to the water supply tube between the column and the chamber. Bands of black plastic tape were attached to the outside of the test chamber wall as an aid to visual orientation of the fish.

#### EXPERIMENTAL PROCEDURE

The procedures followed in experiments with the two species of fish were essentially the same. Five fish of uniform size were taken from the holding tank the day before a test and placed in the test chamber late in the afternoon, the temperature within the apparatus having been previously adjusted. As

soon as the fish were calm, the water velocity was increased to 7.6 cm/sec. At this low water velocity, the fish were able to maintain their positions within the chamber with little or no exertion. The fish were left undisturbed in the apparatus until the next morning (about 16 hr), when the water velocity was gradually increased, in 5 or 15 min, to a base velocity of 15.2 cm/sec in the experiments with largemouth bass and 22.8 cm/sec in those with coho salmon. These two base velocities, especially the first, were not much above the lowest velocities at which the fish had to swim to maintain their positions within the test chamber and avoid impingement on the downstream closure. After the desired water velocity had been reached, the dissolved oxygen concentration was reduced or increased as necessary. The dissolved oxygen content of the water in the chamber reached the desired constant level and the fish learned to swim steadily against the current during a subsequent 4-hr period, after which the water velocity was raised by uniform increments until all five fish failed to continue swimming. Both largemouth bass and coho salmon were subjected to velocity increments of 2.3 cm/sec every 10 min, starting in each case from the stated base velocity.

The free carbon dioxide concentration was adjusted at the same time as the dissolved oxygen concentration in one series of tests with each species of fish. In all other experiments in which the fish were subjected to elevated levels of free carbon dioxide, the carbon dioxide concentration was adjusted before placing the fish in the experimental chamber, but the dissolved oxygen concentration remained near the air-saturation level until the following morning.

In tests with coho salmon, a beam of light from a 60-w incandescent lamp was directed at the downstream end of the chamber to discourage fish from swimming in the immediate vicinity of the movable screen. The downstream closure (retractable screen) was rotated as necessary in order to stimulate all fish that had failed to continue swimming and had come to rest against the closure. The water velocity at which an individual fish apparently had been forced permanently against the screen was recorded as the *final swimming speed* of that fish. The fish was removed with the aid of a small dip net inserted into the test chamber through the funnel-like receptacle and port at the downstream end of the chamber; retraction of the movable screen permitted the current to carry the fish off the screen and into the dip net. After removal, the fish were held separately in 1-liter beakers until termination of the test.

Water temperatures were checked frequently during experiments. The temperature ranges in experiments with coho salmon did not exceed 1.5 degrees C with but four unimportant exceptions. The ranges tended to be greater in the earlier tests with largemouth bass, exceeding 1.5 but not 2.3 degrees C in eight tests, and failures of the thermoregulatory system in two experiments resulted in 3.6 and 2.8 degrees C fluctuations. After the last fish to fail had been removed from the test chamber, samples of water flowing out of the test chamber were taken for chemical analyses. All water analyses were done by standard methods (American Public Health Association, 1960). Dissolved oxygen concentrations near or below the air-saturation level were determined

by the Alsterberg (azide) modification of the Winkler method; the Pomeroy-Kirschman-Alsterberg method was used for determining concentrations far above the air-saturation level. Carbon dioxide levels were determined nomographically, after determining  $pH$ , total alkalinity, temperature, and total dissolved solids. After the water analyses had been completed, the fish were individually measured and weighed, and blood samples usually were taken for hemoglobin determinations.

The hemoglobin content of the blood of the test animals was determined at the ends of most of the tests. The cyanmethemoglobin method, as described by Wintrobe (1961), was employed in all determinations. A 20-lambda sample of blood, obtained by severing the caudal peduncle of a fish, was diluted in 5 ml of Drabkin's solution, which converted the hemoglobin to cyanmethemoglobin; the latter was measured electrophotometrically. A Beckman Model D.U. spectrophotometer was used to measure the optical density of the cyanmethemoglobin solution at a wave length of 540  $m\mu$ . The optical density scale of the spectrophotometer was periodically standardized, using Hemotrol as a hemoglobin standard.

#### EXPERIMENTS ON LARGEMOUTH BASS

Experiments with largemouth bass (Table I) were performed between April 25 and July 25, 1962. All mean weights, and final swimming speeds in Table I are means for five fish except those pertaining to only one test. In that test, the first-failing fish had an injured caudal fin; therefore, the values for the other four fish only were averaged. Data on the individual fish, and also ranges of water temperatures observed during the tests, have been reported by Dahlberg (MS, 1963).<sup>6</sup> The final swimming speed of a fish in lengths per second (L/sec) is a relative speed calculated by dividing the recorded final swimming speed, expressed in centimeters per second, by the total length of the fish in centimeters.

The use of relative swimming speeds of bass (L/sec), rather than absolute speeds (cm/sec), appeared to be decidedly advantageous. The absolute speeds of bass tested at high oxygen and low carbon dioxide concentrations tended to increase with increase of body length. The relative speeds (L/sec), on the other hand, appeared to be independent of body length within the narrow range of lengths represented (75-88 mm).

It is apparent (Fig. 2) that the swimming speed of largemouth bass at low carbon dioxide concentrations decreased with reduction of dissolved oxygen concentration below 5 or 6 mg/liter. At tested oxygen concentrations above 6 mg/liter, the performance of bass apparently was virtually independent of oxygen concentration.

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<sup>6</sup>Some errors to be found in Dahlberg's (MS, 1963) thesis, such as inaccurate determinations of free carbon dioxide levels, were corrected in the course of preparation of the present paper through reference to original (bench) notes and recomputation.

TABLE I. Experimental conditions and the mean sizes and final swimming speeds of juvenile largemouth bass (usually five) in tests at various concentrations of dissolved oxygen and carbon dioxide.

Date of expt.	Mean temp (C)	Mean dissolved oxygen (mg/liter)	Free carbon dioxide <sup>a</sup> (mg/liter)	Total alkalinity <sup>b</sup> (mg/liter)	pH	Mean total length (mm)	Mean weight (g)	Mean final swimming speed	
								cm/sec	L/sec
4/25/62	24.7	8.40	—	—	—	80.8	4.86	37	4.6
4/26/62	25.1	5.20	—	—	—	81.8	5.52	40	4.9
4/27/62	25.2	2.20	—	—	—	83.0	6.04	33	4.0
4/28/62	25.1	6.40	—	—	—	84.6	6.20	41	4.9
4/29/62	24.8	13.30	—	—	—	84.0	5.54	38	4.5
4/30/62	25.2	1.40	—	—	—	81.2	5.24	25	3.1
5/1/62	25.1	3.50	—	—	—	80.4	5.31	36	4.5
5/5/62	24.9	11.40	—	—	—	82.4	6.10	41	5.0
5/8/62	25.1	1.00	—	—	—	82.0	5.95	20	2.4
5/9/62	25.0	19.70	—	—	—	81.6	5.78	40	5.0
5/10/62	24.9	4.50	—	—	—	80.8	5.69	38	4.7
5/11/62	24.9	3.00	—	—	—	81.4	5.68	36	4.4
5/14/62	24.9	10.30	—	—	—	82.8	6.03	39	4.7
5/15/62	25.2	4.30	—	—	—	83.2	6.36	36	4.4
5/16/62	25.1	2.50	—	—	—	81.2	5.80	31	3.8
5/17/62	24.9	6.60	—	—	—	81.4	6.01	37	4.6
5/18/62	24.8	1.50	—	—	—	82.2	5.66	27	3.3
5/23/62	25.0	24.00	—	—	—	82.8	6.39	37	4.7
5/24/62	25.1	7.60	—	—	—	81.8	5.72	37	4.5
6/26/62	25.0	8.10	2.5	85	7.80	79.6	5.58	40	5.0
7/4/62	25.1	4.70	—	—	—	81.2	5.81	38	4.6
7/5/62	25.0	3.10	—	—	—	81.2	5.94	36	4.5
7/10/62	25.0	7.90	25	94	6.85	82.8	6.11	40	4.8
7/11/62	24.9	3.30	38	92	6.65	81.8	6.13	37	4.5
7/12/62	25.3	2.10	24	—	6.85	82.2	6.31	35	4.2
7/13/62	24.9	1.35	28	94	6.80	81.8	6.45	29	7.8
7/16/62	24.9	5.10	26	96	6.80	86.2	7.36	43	5.0
7/17/62	23.4	1.85	44	—	6.60	83.0	6.20	30	3.7
7/18/62	24.8	7.85	43	96	6.60	83.0	6.32	41	4.8
7/19/62	24.8	3.20	49	—	6.55	83.6	6.25	38	4.5
7/20/62	24.8	5.10	54	—	6.50	83.6	6.41	40	4.7
7/24/62	25.0	2.10	18*	—	7.00	81.8	5.82	32	3.9
7/25/62	24.1	1.20	23*	97	6.90	83.4	6.11	24	2.8
7/26/62	25.1	4.40	22*	—	6.90	85.2	6.82	40	4.7

<sup>a</sup>An asterisk (\*) indicates that fish were not acclimated to the carbon dioxide concentration shown. A dash (—) indicates that carbon dioxide was not added to the stream water and the low concentration of free CO<sub>2</sub> in the water was not evaluated (pH not determined).

<sup>b</sup>Bicarbonate alkalinity expressed as calcium carbonate (CaCO<sub>3</sub>) equivalent. Determinations of total dissolved solids ranged between 130 and 133 mg/liter.

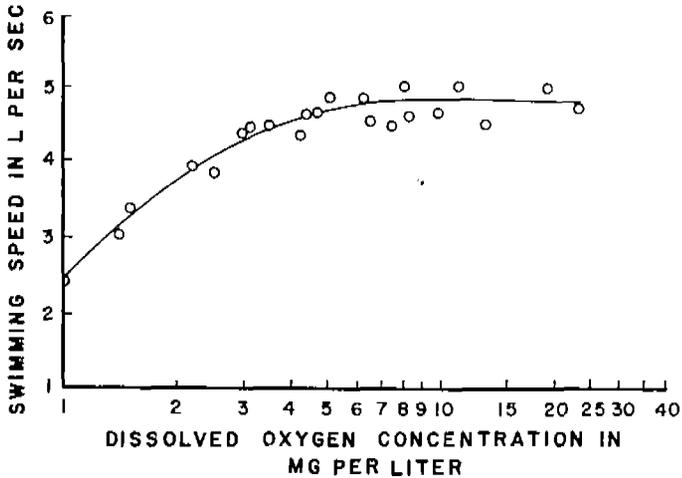


FIG. 2. Relationship between the mean final swimming speed of largemouth bass, expressed in L/sec, and the dissolved oxygen concentration at nearly natural, low concentrations of carbon dioxide (probably <3 mg/liter) and temperatures near 25 C.

Free carbon dioxide concentrations were not determined during the tests whose results are plotted in Fig. 2, with but one exception. Determinations made under similar experimental conditions during the same season of the next year (the spring of 1963) indicated that free carbon dioxide concentrations probably never exceeded 3 mg/liter during the test period.

Figure 3 facilitates comparison of the results of the different kinds or groups of experiments performed with largemouth bass. In the group of tests in which the concentrations of free carbon dioxide averaged 21 mg/liter, the fish were exposed to them for little time before the swimming performance trials, the carbon dioxide concentration having been increased at the same time that the dissolved oxygen concentration was reduced. The data to which the curve was fitted are not shown in Fig. 3, except three points (solid triangles) that represent data obtained later than the rest and at about the time that the tests at elevated carbon dioxide concentrations were performed. The individual test data from the latter experiments are all included in Fig. 3, and most of them do not deviate markedly from the curve. Those that do deviate considerably are above the curve, and not below, indicating improvement of swimming performance. However, since all of the three points based on tests at low carbon dioxide concentrations (solid triangles) also fall above the curve, it appears that the bass probably were generally able for some reason to perform slightly better in the later tests than in the earlier ones under the same conditions. Thus, it can be concluded that concentrations of free carbon dioxide even above 40 mg/liter, which are rarely found in nature, had virtually no adverse effect on the swimming performance of bass, but there is not sufficient evidence of improvement of the performance at any concentration of carbon dioxide.

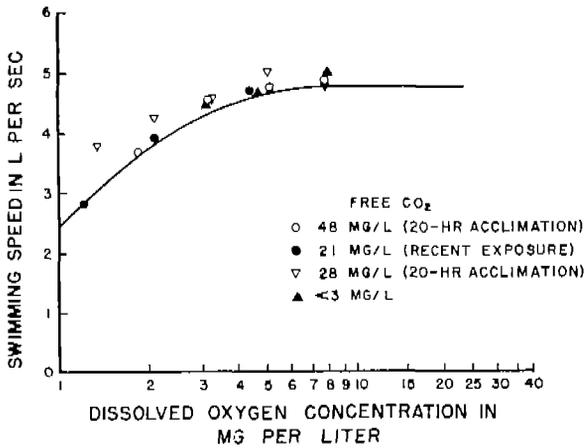


FIG. 3. Mean final swimming speeds, expressed in L/sec, of largemouth bass at various concentrations of dissolved oxygen and carbon dioxide. The curve relating swimming speed to oxygen concentration is the curve that was fitted to all data from tests at the low concentration of free carbon dioxide (probably <3 mg/liter) only, most of which (those from early tests) have not been plotted here. The stated free carbon dioxide levels of 48, 21, and 38 mg/liter are means of observed values for individual tests ranging from 44 to 55 mg/liter, 17 to 23 mg/liter, and 24 to 38 mg/liter, respectively. See text for further details.

There was not much difference in performance between the first-failing and third-failing bass, and the data pertaining to each do not deviate widely from the respective cyc-fitted curves (Fig. 4).

Hemoglobin determinations were made on blood samples from 67 juvenile largemouth bass used in the performance tests, none having been made in the earliest tests. The mean and standard deviation of the values obtained (Dahlberg, MS, 1963) are 7.92 and 0.47 g/100 ml, respectively.

#### EXPERIMENTS ON COHO SALMON

Experiments with coho salmon (Table II) were performed between August 6 and November 9, 1962, and between October 20 and December 10, 1964. Data on individual fish tested in 1962 have been reported by Dahlberg (MS, 1963).<sup>6</sup> Five fish were used in each test and the final swimming speed (also length and weight) was recorded for each of the five fish except in seven tests in which only four terminal speeds were recorded, and one test in which three final speeds were noted. In seven of the excepted tests, one or two fish (two

<sup>6</sup>As noted earlier, some errors to be found in Dahlberg's (MS, 1963) thesis, such as inaccurate determinations of free carbon dioxide, were corrected in the course of preparation of the present paper. These errors include the recording of the fork lengths of coho salmon used in experiments No. 61 through 77 as total lengths.

TABLE II. Experimental conditions and the mean sizes and final swimming speeds of juvenile coho salmon (usually five) in tests at various concentrations of dissolved oxygen and carbon dioxide. See text for further details.

Date of expt.	Mean temp (C)	Mean dissolved oxygen (mg/liter)	Free carbon dioxide <sup>a</sup> (mg/liter)	Total alkalinity <sup>b</sup> (mg/liter)	pH	Mean total length <sup>f</sup> (mm)	Mean weight (g)	Mean final swimming speed		Mean adjusted final swimming speed <sup>d</sup> (L/sec) <sup>e</sup>
								cm/sec	L/sec <sup>e</sup>	
8/6/62	20.1	9.50	1.9	-	8.00	84.4	4.97	54	6.4	6.5
8/7/62	19.8	4.75	2.6	95	7.85	83.2	4.65	51	6.1	6.2
8/9/62	20.0	9.60	58	-	6.50	85.6	4.99	44	5.2	5.3
8/10/62	20.0	4.60	58	95	6.50	80.6	4.51	41	5.1	5.0
8/13/62	20.0	17.50	1.7	-	8.05	80.0	4.63	58	7.2	7.1
8/14/62	20.1	6.10	1.4	103	8.15	81.6	4.71	54	6.6	6.6
8/15/62	19.9	11.70	1.4	103	8.15	92.0	6.62	60	6.5	7.0
8/16/62	19.7	3.40	1.5	103	8.18	86.6	5.59	39	4.5	4.7
8/17/62	20.0	25.70	1.5	102	8.18	83.8	4.99	58	6.8	6.9
8/20/62	19.9	2.20	1.5	104	8.18	84.0	4.89	32	3.8	3.9
8/21/62	20.0	2.70	45	100	6.65	81.6	4.70	36	4.4	4.4
8/22/62	19.9	24.90	50	-	6.60	80.8	4.43	49	6.1	6.0
8/23/62	20.0	6.80	40	101	6.70	77.8	3.96	49	6.4	6.2
8/24/62	20.0	7.20	1.6	-	8.10	85.0	5.14	61	7.1	7.3
8/27/62	20.3	2.10	2.1	100	7.95	84.8	5.09	28	3.3	3.3
9/4/62	20.3	2.10	41	103	6.68	85.2	5.51	31	3.6	3.7
9/5/62	20.0	15.30	46	-	6.65	92.6	6.93	56	6.1	6.6
9/6/62	20.0	6.10	18	-	7.05	88.6	5.86	56	6.3	6.6
9/7/62	20.0	9.20	18	-	7.05	82.0	4.77	57	7.0	7.0
9/8/62	20.0	4.50	18	-	7.05	80.6	4.40	50	6.2	6.2
9/9/62	20.0	22.80	18	-	7.05	81.6	4.53	58	7.0	7.0
9/10/62	19.9	3.70	17	104	7.10	80.6	4.36	45	5.6	5.5
9/11/62	19.9	2.80	2.5	-	7.90	79.6	4.29	39	4.9	4.9
9/14/62	20.1	20.15	2.3	-	7.95	77.6	3.97	60	7.7	7.5
9/15/62	20.0	5.20	2.3	-	7.95	80.4	4.43	54	6.6	6.6
9/16/62	20.1	2.00	2.0	-	8.00	86.4	5.23	33	3.8	3.9
9/17/62	20.0	7.50	2.0	-	8.00	85.2	5.13	64	7.4	7.5
9/18/62	20.1	10.35	2.5	-	7.92	88.8	5.86	66	7.4	7.7
9/19/62	20.1	4.20	2.8	100	7.85	86.0	5.09	54	6.3	6.5
9/22/62	20.0	15.20	20	100	7.00	84.0	4.97	57	6.8	6.9

9/23/62	20.3	2.00	16	100	7.10	81.5	4.63	32	3.9	3.9
9/24/62	20.2	9.60	18*	-	7.05	78.3	3.98	51	6.6	6.4
9/25/62	19.4	4.80	18*	-	7.05	81.6	4.00	47	5.7	5.7
9/28/62	20.0	3.70	2.2	80	7.85	81.0	4.33	43	5.3	5.3
9/30/62	20.1	17.00	18*	98	7.05	75.6	3.51	44	5.9	5.6
10/1/62	20.0	3.30	16*	-	7.10	77.4	3.92	41	5.2	5.1
10/2/62	20.0	6.90	16*	-	7.10	80.0	4.00	53	6.6	6.5
10/3/62	20.0	2.60	20*	-	7.00	76.8	3.65	36	4.7	4.5
11/2/62	20.0	3.80	2.0	-	8.00	79.8	3.99	47	5.8	5.8
11/3/62	20.0	13.90	18*	99	7.05	81.8	4.14	57	6.9	6.9
11/4/62	20.0	2.70	16	99	7.10	80.8	4.06	37	4.5	4.5
11/5/62	20.2	2.55	2.2	-	7.95	83.0	4.66	38	4.5	4.5
11/6/62	20.2	17.60	39	99	6.70	86.6	5.11	60	7.0	7.2
11/9/62	20.1	17.80	3.2	-	7.80	82.0	4.67	64	7.8	7.8
10/21/64	18.3	9.75	1.8	106	8.10	84.6	5.00	60	7.1	7.3
10/22/64	20.3	9.00	1.7	102	8.10	81.4	4.31	58	7.1	7.1
10/28/64	19.7	8.90	68	102	6.50	82.0	4.65	49	5.9	5.9
10/29/64	19.8	4.90	60	110	6.60	82.0	4.48	47	5.9	5.9
10/30/64	20.0	5.05	2.2	102	7.95	81.4	4.25	52	6.4	6.4
11/3/64	20.2	2.78	2.2	92	7.95	82.8	4.77	39	4.7	4.7
11/4/64	20.1	2.80	55	88	6.55	82.0	4.61	35	4.3	4.3
11/6/64	19.9	14.70	65	98	6.40	82.8	4.75	51	6.1	6.2
11/7/64	20.1	18.10	1.5	-	8.00	81.8	4.75	61	7.4	7.4
11/12/64	20.0	19.80	62	74	6.35	82.0	4.58	54	6.6	6.6
11/13/64	20.0	2.25	70	-	6.40	82.0	4.80	33	4.0	4.0
11/17/64	20.2	2.30	2.0	94	7.95	82.0	4.73	35	4.3	4.3
11/20/64	20.0	24.10	64	100	6.50	80.0	4.34	53	6.6	6.5
11/24/64	19.8	6.55	120	80	6.20	82.2	4.80	50	6.1	6.1
11/25/64	19.8	24.45	3.8	56	7.60	82.0	4.65	57	7.0	7.0
12/1/64	19.9	6.40	2.2	40	7.50	81.5	4.56	58	7.1	7.1
12/4/64	20.1	12.50	3.0	50	7.50	82.0	4.82	62	7.5	7.5
12/8/64	20.0	11.20	95	52	6.10	82.2	4.50	54	6.5	6.5
12/10/64	20.1	21.50	66	54	6.20	80.4	4.61	51	6.3	6.2

<sup>a</sup>An asterisk (\*) indicates that fish were not acclimated to the carbon dioxide concentration shown.

<sup>b</sup>Bicarbonate alkalinity expressed as calcium carbonate (CaCO<sub>3</sub>) equivalent. Determinations of total dissolved solids ranged between 160

and 198 mg/liter.

<sup>c</sup>The total lengths (TL) of the salmon in mm were computed from the measured fork lengths (FL) by an appropriate conversion formula

(TL = 1.0804FL + 0.13).

<sup>d</sup>Size-adjusted for a uniform total body length of 82 mm.

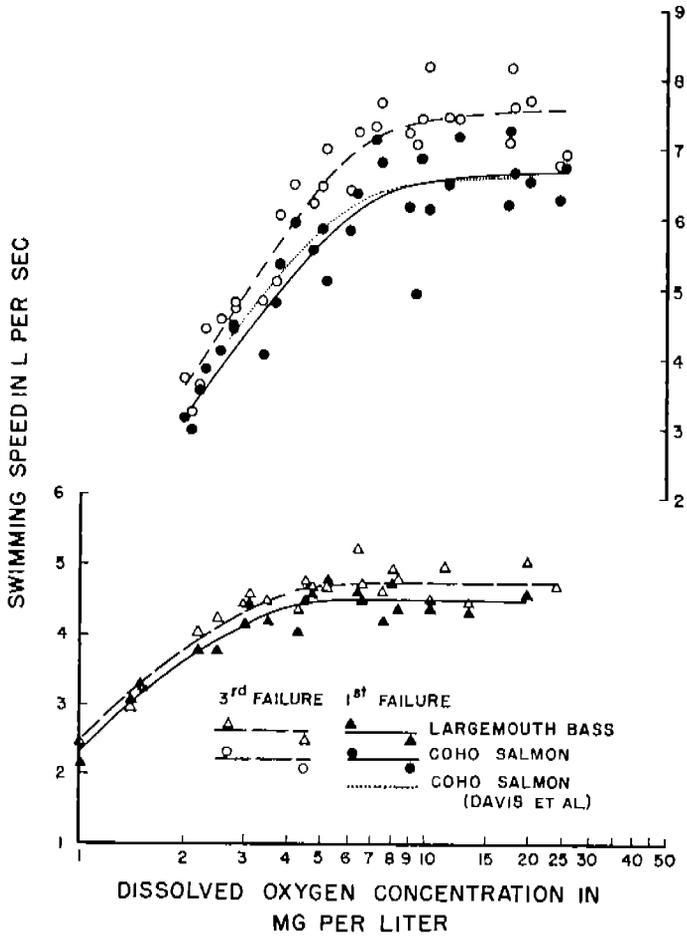


FIG. 4. Final swimming speeds, in L/sec, of first-failing and third-failing (of five) coho salmon and largemouth bass at low concentrations ( $<3$  mg/liter) of carbon dioxide in relation to the dissolved oxygen concentration. The swimming speeds of the coho salmon were adjusted (size-corrected) for a total length of 82 mm in the manner explained in the text. The curve based on the data of Davis et al. (1963) is shown without the individual observations to which it was fitted. It relates the adjusted final swimming speeds at 20 C of first-failing coho salmon to oxygen concentration. Inasmuch as observations pertaining to failures at the base velocity are of questionable value (Davis et al., 1963), such an observation at an oxygen concentration of about 1.5 mg/liter was discarded in plotting the latter curve. All curves were fitted by eye.

in one test only) remained in a favorable position near the baffles at the upstream end of the test chamber. These fish were thus seemingly able to withstand water velocities much higher than the terminal velocities recorded for other fish tested. In one test a fish found to have frayed fins was disregarded. In most experiments the fish did not find the favorable positions described,

and all five final swimming speeds were used in computing the means. In experiments reported by Davis et al. (1963), chinook salmon often derived advantage from the eddies behind the baffles, but coho salmon did so only rarely.

The relative swimming speeds in L/sec were adjusted (size-corrected for a total body length of 82 mm) so as to compensate for difference of the fish in size only, which is known to influence both the absolute swimming speed (in cm/sec) and the relative speed (in L/sec). When the total length of a fish was greater than 82 mm (mean length of all the coho salmon used), the adjustment was made by taking the logarithm of the observed swimming speed of a fish in L/sec, adding a value equal to 0.0027 times the difference between 82 mm and the actual length of the fish in mm, and then finding the antilogarithm of the sum. When the length of the fish was less than 82 mm, a corresponding adjustment was made by subtraction.

According to unpublished data obtained in our laboratory by E. M. Smith, Jr., the logarithm of the final relative swimming speed of juvenile coho salmon in L/sec declines almost linearly by about 0.0027 with increase in total length of the fish by 1 mm within the length range of 70-120 mm. Our own data are in fair agreement with this finding, which is based on results of numerous tests at high oxygen and low carbon dioxide concentrations performed by Smith with our apparatus and by methods similar to ours. The above relationship does not hold for salmon much less than 70 mm in length, and it obviously cannot apply to fish much more than 120 mm long. Smith's data on sustained speeds do not agree well with the linear relationship suggested by Bainbridge (1960) between the logarithm of body length of a fish and the logarithm of the maximum absolute swimming speed sustainable for a relatively short time interval (burst speed). Bainbridge's method of speed adjustment for differences in body length was therefore rejected in favor of the above-described method. Within the range of lengths of our coho salmon (74-100 mm), the decrease of their relative sustained swimming speed (L/sec) with increase of body length is about as great, proportionally, as is the increase of the absolute speed (cm/sec). Thus, the computation and use of unadjusted relative speeds is not decidedly advantageous in the case of the coho salmon, as it appeared to be in the case of the largemouth bass. Nevertheless, it was decided to express adjusted speeds of coho salmon in L/sec, rather than in cm/sec, so that the data for salmon and bass plotted in our figures would be comparable.

In Fig. 5, the points representing results of the two tests at carbon dioxide concentrations above 70 mg/liter (95 and 120 mg/liter) are given as solid circles; the 16 others of the same group represent results of tests at concentrations ranging from 39 to 70 mg/liter and averaging 55 mg/liter. All but one of the tests at concentrations ranging from 39 to 58 mg/liter (mean 48 mg/liter) were performed in 1962, and all tests at concentrations of 60 mg/liter and more (mean 74 mg/liter) were performed in 1964. Surprisingly, there was no evident difference between the results obtained in these two series of tests, so that one curve fits all of these data reasonably well. Even

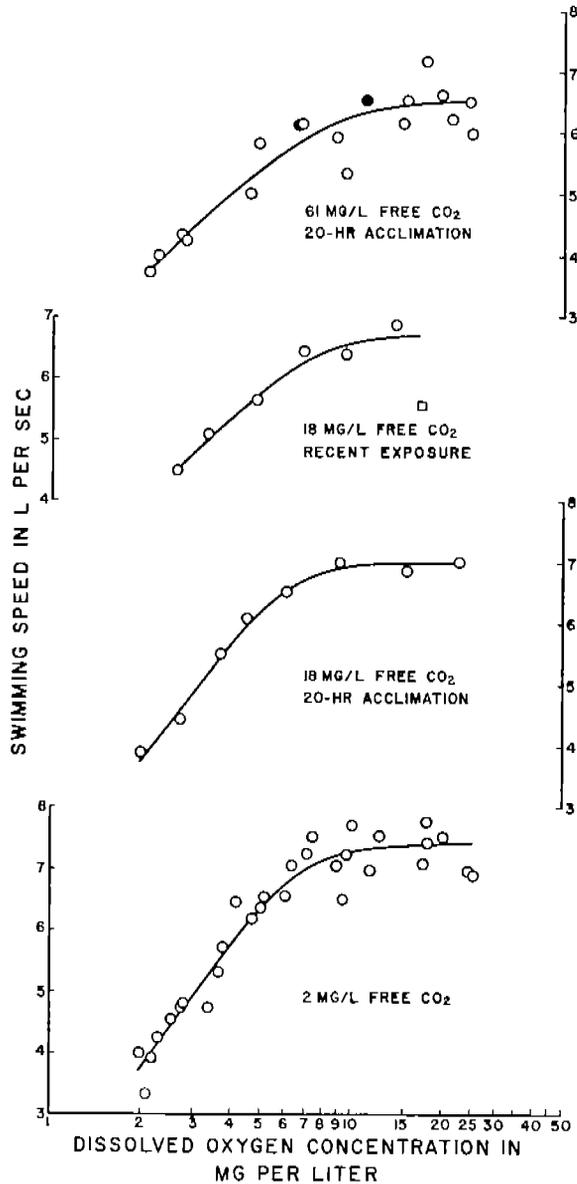


FIG. 5. Mean adjusted (size-corrected for a total length of 82 mm) final swimming speeds of coho salmon at different mean levels of free carbon dioxide in relation to dissolved oxygen concentration. The solid circles represent results of two tests at the very high carbon dioxide concentrations of 95 and 120 mg/liter. For fish recently exposed to 18 mg/liter free CO<sub>2</sub>, the single square represents an anomalous result that was disregarded in fitting the curve to the other observations even though we are not aware of any fault of the test (at 17 mg/liter dissolved oxygen) that would account for the low mean final swimming speed of the fish. The stated free carbon dioxide levels of 61, 18, and 2 mg/liter are means of observed values for individual tests ranging from 39 to 120 mg/liter (with only two values above 70 mg/liter), 16 to 28 mg/liter, and 1.4 to 3.8 mg/liter, respectively. The curves were fitted by eye. See text for further details.

the two points obtained in 1964 at carbon dioxide concentrations of 95 and 120 mg/liter are close to the curve and slightly above it.

Between dissolved oxygen concentrations of about 2 mg/liter and 7 or 8 mg/liter, the swimming speed of the coho salmon declined markedly and almost linearly with decrease of the logarithm of the dissolved oxygen concentration (Fig. 5). Within the range of tested dissolved oxygen concentrations above 9 mg/liter, variation of oxygen concentration had only a slight effect on the swimming performance.

Figure 6 facilitates comparison of the curves shown in Fig. 5. Except at more or less reduced oxygen concentrations, elevated carbon dioxide concentrations near 18 mg/liter apparently influenced the final swimming speed

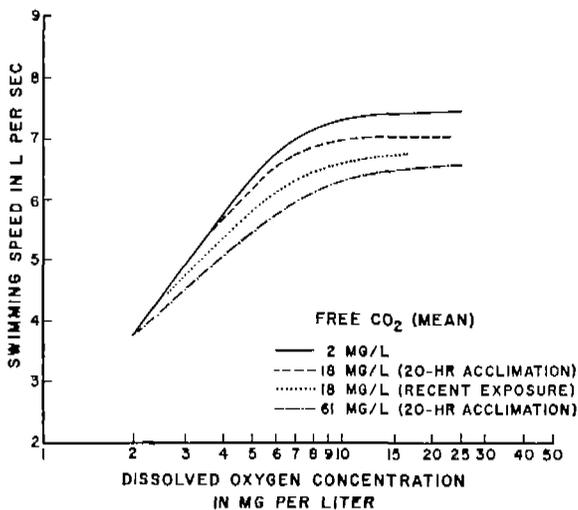


FIG. 6. Comparison of curves (from Fig. 5) relating mean adjusted (size-corrected for a total length of 82 mm) final swimming speeds of coho salmon to dissolved oxygen concentration obtained at different mean levels of free carbon dioxide.

of coho salmon, especially when the fish had not become adjusted to them. Even after overnight acclimation, free carbon dioxide concentrations ranging from 39 to 120 mg/liter and averaging 61 mg/liter evidently had a pronounced effect on the swimming speed, but only at dissolved oxygen concentrations well above 2 mg/liter. At the 2 mg/liter level of dissolved oxygen, no effect of the high free carbon dioxide concentration was apparent, and the greatest effect occurred at an oxygen concentration near and above 6 mg/liter. When oxygen concentrations were above 6.0 mg/liter, 11 of 12 tests at the highest carbon dioxide concentrations yielded mean adjusted final swimming speeds below 6.8 L/sec, whereas 14 of 16 tests at the lowest carbon dioxide concentrations yielded mean values above 6.8 L/sec (Fig. 5). Thus, there can be

little doubt that the difference between the curves obtained for the highest and lowest carbon dioxide concentrations (Fig. 6) is not fortuitous. The expected, intermediate positions of the two curves obtained at intermediate carbon dioxide concentrations averaging 18 mg/liter should be considered as confirmatory evidence.

A rather marked difference can be seen between the swimming speeds of first-failing and third-failing coho salmon (Fig. 4). There is very little difference between the curves based on first-failure data reported here and the first-failure data reported by Davis et al. (1963), who used underyearling coho salmon of about the same size as those used in our study and recorded first and second failures only. The differences between final swimming speeds of our first-failing and third-failing fish probably were due to persistent differences in swimming ability of individual fish like those found by Thomas et al. (1964) through retesting of groups of juvenile salmonids. Our fish were not retested, however, to determine whether or not the same individuals consistently show poor or good performance in repeated trials.

Hemoglobin determinations were made on blood samples from 184 coho salmon (in all but five tests) in 1962, but none in 1964. The mean and the standard deviation of the values obtained (Dahlberg, MS, 1963) are 6.85 and 0.82 g/100 ml, respectively.

#### DISCUSSION

The swimming speeds sustained by fish for 10 min that are reported here as final swimming speeds suitable for our comparative purposes are not necessarily speeds sustainable indefinitely. Brett (1964) has considered, with attention to pertinent earlier literature, the duration of tests necessary for measuring the true sustained swimming capacity of fish, as indicated by the relation between swimming velocity and fatigue time. On the basis of his own limited data, he concluded that "for sockeye [salmon] a reliable estimate of sustained speed could not be obtained under a test period of about 5 hr." More extensive unpublished data on coho salmon recently obtained in our laboratory by E. M. Smith provide no support for a 5-hr test period but considerable justification for a test period of about 30-50 min. However, they also show that the ability of an individual coho salmon to maintain a certain speed for an hour, or even for 5 hr, does not signify that its failure to maintain that speed cannot occur soon thereafter. Furthermore, practical considerations precluded the use of time intervals much greater than 10 min between velocity increments in our tests. The 10-min intervals somewhat arbitrarily chosen by Davis et al. (1963) therefore were adopted also in our work, facilitating comparison of our results with those of the latter authors. Having used 20-min time intervals between velocity increments instead of 10-min intervals in a few tests performed for comparative purposes, Davis et al. (1963) did not find that the doubling of the length of the intervals results in appreciable decrease of final swimming speeds of coho salmon. Thus, 10-min intervals may prove entirely justifiable when the velocity increments are as small as ours.

High concentrations of free carbon dioxide had a more pronounced effect on the swimming speed of coho salmon at dissolved oxygen concentrations near or above the air-saturation value than at oxygen concentrations far below air-saturation (Fig. 6). This observed difference in effectiveness of carbon dioxide at different dissolved oxygen levels will be considered in the light of available information concerning the influence of the gas on the affinity of fish blood for oxygen.

A notable characteristic of fish blood is its very incomplete oxygenation even at extremely high oxygen tensions in the presence of moderate amounts or tensions of carbon dioxide. The large effect of carbon dioxide on the affinity of blood for oxygen at high oxygen tensions was first noted in several species of marine fish by Root (1931), and it is often called the Root effect, though it may be regarded by some as inseparable from the well-known Bohr effect. The Root effect has been observed in salmonid fishes (Ferguson and Black, 1941; Black et al., 1966a, b, c, d).

With increasing activity of a fish, the oxygen requirement of its tissues increases. The intensity of sustained activity therefore may, under some conditions, be limited by the ability of the blood to transport oxygen to the tissues. It can also be limited by the rate of delivery of oxygen to the blood at the gills when this rate is insufficient for full utilization of the oxygen transport capacity of the blood. There may be other limiting factors.

We do not yet know whether the final swimming speed of healthy (not anemic) salmon at normal carbon dioxide concentrations and high dissolved oxygen levels at which the speed is virtually independent of oxygen concentration is or is not limited by the oxygen transport capacity of their blood. Davis et al. (1963) and Brett (1964) have discussed the factors that may limit swimming speeds and oxygen uptake rates of salmon. They have arrived at no definite conclusion that can be regarded as an answer to the above question. Basu (1959) perhaps unjustifiably equated the maximum oxygen uptake rate of active fish in well-oxygenated water to "the ability of the fish to transport oxygen from the external medium under activity". He found no direct relation between the effects of carbon dioxide on the "active" oxygen uptake rates of various fish at high oxygen concentrations and its effects on the ability of their bloods to take up oxygen. Nevertheless, it seems reasonable to suppose that the level of activity that coho salmon can maintain at high oxygen concentrations in the ambient medium may be reduced by carbon dioxide at least in part through reduction of the ability of the blood to transport oxygen.

As the concentration of oxygen decreases from a high level in water whose carbon dioxide content is not too high, extraction by active fish of sufficient oxygen from the water may be maintained by passing enough water over the gills. However, after a point has been reached where the greatest possible irrigation of the gill surfaces can barely supply enough oxygen for nearly complete oxygenation of the blood, the level of sustainable activity must decrease with further reduction of dissolved oxygen. At low oxygen concentrations, the maximum sustainable activity is believed to be mostly or entirely

determined by the maximum possible rate of gill irrigation; the blood's largely unutilized oxygen transport capacity would not be truly limiting, though it may have some indirect import (Davis et al., 1963). Therefore, it appears that the effect of moderately high carbon dioxide concentrations on the ability of the blood to transport oxygen, which effect may be very important at high oxygen concentrations, should be less important or of no consequence, in relation to swimming performance, at low oxygen concentrations. At a low oxygen concentration, the extent of oxygenation of the blood at the gills is a function of the amount of oxygen delivered to the gills, and the amounts of oxygen taken up at the gills by bloods having normal and reduced affinities for oxygen therefore need not necessarily differ materially.

It must be admitted that the above explanation of our finding can be reasonably criticized as an extreme oversimplification of a complex problem; when it is pressed, some serious weaknesses or difficulties become apparent. Oxygen moves at the gills from the ambient medium into the blood plasma and thence into erythrocytes at varying rates dependent on diffusion gradients maintained by gill irrigation and tissue respiration. The oxygen content of blood returning to the gills depends on the degree of discharge of oxygen from the blood to the respiring tissues, also by diffusion. The rates of both the loading of the blood with oxygen and its unloading must be influenced by carbon dioxide. Equilibria like those on which oxygen dissociation curves for blood are based probably are never directly involved in the operation of the complex and dynamic system under consideration here. It is evident that only at very high oxygen tensions of the external medium is nearly full utilization possible of the oxygen capacity of the blood of a very active coho salmon when little carbon dioxide is present. Much lower tensions doubtless would suffice for full oxygenation of the blood's hemoglobin upon attainment of equilibrium.

Still, the reduction by carbon dioxide of the affinity of the bloods of salmonids for oxygen that has been reported must result in reduction of the degree of oxygenation of these bloods when the fish are swimming rapidly in water with very high oxygen tensions. Also, the fact remains that the maximum swimming speeds of our coho salmon at low and high carbon dioxide concentrations were virtually equal when the dissolved oxygen level was very low. We can conclude that there was no material effect of carbon dioxide on the amount of oxygen that could be extracted by the fish from the oxygen-deficient water passing over their gills. Thus, it appears that the proposed explanation of our results, or of the convergence of the curves in Fig. 6 on the left side, may be essentially sound.

An alternative, tentative explanation of our finding could be based on the supposition that carbon dioxide somehow depresses internal (tissue) respiration of active coho salmon and their muscular power more directly than through its influence on the oxygen-carrying ability of their blood, and independently of that influence. Such an effect also could well become less important and finally disappear under hypoxial conditions as the oxygenation

of the blood at the gills and the supply of oxygen to the tissues are reduced. Possible inhibition of activities of some enzymes essential to maintenance of muscular function should be relatively ineffective when the oxygen supply to muscle and other tissues is highly deficient and severely restricts tissue respiration. The importance of the effect of carbon dioxide on blood and oxygen transport perhaps has been overemphasized in the past.

Our incidental observation that a large increase of free carbon dioxide from about 50 (39–60) mg/liter to about 100 (95–120) mg/liter had no apparent effect on the swimming performance of coho salmon at rather high oxygen concentrations (Fig. 5) is interesting. Such increases of carbon dioxide concentration have a much greater effect on dissolved oxygen lethal thresholds (asphyxial levels) for coho salmon than do increases of free carbon dioxide from low levels to 50 mg/liter (McNeil, MS, 1956). However, Root (1931) found that increases of carbon dioxide beyond certain levels had little or no effect on the affinity for oxygen of the bloods of some marine fishes, and the same has been found to be true of the blood of a salmonid fish (Black et al., 1966d). The noted behavior of blood *in vitro* could help to explain our concordant finding pertaining to the swimming speeds of coho salmon, if that finding can be verified. The agreement of the two kinds of data could then be cited as evidence supporting the supposition that the swimming speed of coho salmon in our tests at high concentrations of both oxygen and carbon dioxide was limited by the ability of the blood to transport oxygen.

Basu (1959) found that the logarithms of the "active" oxygen consumption rates of fish at all oxygen concentrations generally decrease linearly with increase of free carbon dioxide concentration from zero. Carbon dioxide usually had about as much effect on these rates at moderately reduced oxygen concentrations as at high concentrations. Its effect on the "active" oxygen uptake rates of three tolerant species of warmwater fish was considerably greater at very low concentrations than at higher concentrations.<sup>7</sup> The apparent disagreement of Basu's findings with our observation that carbon dioxide had little or no effect on the swimming speed of coho salmon at low oxygen concentrations is noteworthy and puzzling. The maximum sustained swimming speed of fish and their maximum oxygen uptake rate at any given temperature are generally assumed to be closely related (Fry, 1957). The lack of any demonstrable impairment of the swimming performance of our largemouth bass by rather high carbon dioxide concentrations at any dissolved oxygen level

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<sup>7</sup>The lowest level of dissolved oxygen at which tests with brook trout, *Salvelinus fontinalis*, the only salmonid tested by Basu (1959), were performed was about 5 mg/liter (44% of air-saturation at the test temperature of 10 C), and no marked difference was observed in effects of carbon dioxide at this and higher oxygen concentrations. At the lowest oxygen concentration tested, the trout lost its ability to be active at a carbon dioxide level somewhat above 50 mg/liter, but maintained a nearly constant oxygen uptake rate with increase of free carbon dioxide up to 80 mg/liter. Some of Basu's "active" oxygen uptake rates for warmwater fish tested at very low oxygen concentrations or at high carbon dioxide concentrations appear to be much less than "standard" or "minimum resting" rates for the same fish species under more favorable conditions. It is not clearly stated that the fish in question were not actually swimming steadily, but they probably were incapacitated and inactive.

(Fig. 3) is interesting in view of the pronounced influence of low concentrations of carbon dioxide on the oxygen uptake rates of other warmwater species reported by Basu (1959).

Our evidence that the effect of free carbon dioxide on the swimming performance of coho salmon decreases markedly with acclimation (Fig. 6) is not deemed conclusive. However, it is in agreement with the findings of other investigators, who noted that the effects of moderate (tolerable) increases of carbon dioxide concentration on the ability of fish to extract oxygen from their medium are largely or entirely transitory (McNeil, MS, 1956; Saunders, 1962; Doudoroff and Warren, 1965). And even our relatively unacclimated (least acclimated) coho salmon had been exposed to the elevated carbon dioxide concentration (about 18 mg/liter) for some time before their swimming performance was measured; without such acclimation, the performance perhaps would have been impaired much more than it was.

In the presence of much dissolved oxygen, the final swimming speeds of largemouth bass at 25 C were generally less than those of coho salmon of about the same size at 20 C. However, had a single vertical scale been used in plotting the data for largemouth bass and coho salmon in Fig. 4, the comparable curves for the two species would have met or intersected, showing the bass to be better swimmers than the coho salmon at dissolved oxygen concentrations below 2 mg/liter. Figure 4 shows that the median final swimming speed of coho salmon (i.e. the final speed of third-failing fish) at the dissolved oxygen concentration of 3 mg/liter is less than the corresponding speed at the air-saturation level of dissolved oxygen by about 30%, whereas the speed of largemouth bass at the 3 mg/liter level is less than the speed at the air-saturation level of dissolved oxygen by only about 10%. Reduction of the sustained swimming speed of largemouth bass (median final speed) by 30%, from the speed at the air-saturation level of dissolved oxygen, can be seen to occur at an oxygen concentration near 1.5 mg/liter. The curves based on mean final swimming speeds in Fig. 2 and 5 differ very little from the corresponding curves in Fig. 4 based on median final speeds.

It is interesting to note that the growth rate of largemouth bass kept on unrestricted food rations at 26 C and low carbon dioxide levels decreases materially with decrease of oxygen concentration from the air-saturation level to 5 or 6 mg/liter (Stewart et al., 1967), whereas the sustained swimming speed of our bass (Fig. 2) did not. This observation may be viewed as an indication that the swimming speed of the bass at high oxygen concentrations was not limited by the oxygen transport capacity of their blood (which seemingly could not be fully utilized at the reduced oxygen concentrations in the experiments on growth) and the supply of oxygen to their tissues. However, its significance is uncertain, for the oxygenation of blood at the gills may be more rapid in very rapidly swimming bass than in heavily fed and relatively quiet bass. The accelerated oxygenation of blood could make possible nearly full utilization of the blood's transport capacity at relatively low dissolved oxygen levels in the active bass consuming oxygen at a maximal rate. Saunders (1962)

has suggested that rapid swimming may even interfere with the respiration of fish, reducing the respiratory volume, but no conclusive evidence was presented.

The sustained swimming speed of coho salmon was not much affected at considerably reduced oxygen concentrations by 18 mg/liter of carbon dioxide after some acclimation (Fig. 6); that of somewhat acclimated largemouth bass was not adversely affected even by 48 mg/liter of carbon dioxide (Fig. 3). Ellis (1937) determined free carbon dioxide concentrations in various American rivers and found that they generally did not exceed 14 mg/liter in polluted as well as unpolluted river waters. Alabaster et al. (1957) have stated that carbon dioxide concentrations up to 50 ppm have been observed in a stream containing sewage effluent. The dissolved oxygen content of the water was not stated. Stream waters polluted with mineral acids conceivably could have temporarily even much higher concentrations of liberated carbon dioxide. However, in natural and polluted waters that are not seriously deficient in dissolved oxygen, concentrations of free carbon dioxide certainly do not often approach even 20 mg/liter. The results of our experiments thus do not indicate that free carbon dioxide can often materially impair the swimming performance of freshwater fish in nature. It should be noted, however, that greater effects of carbon dioxide on swimming performance perhaps would have been found had the test temperature been much lower. Coho salmon in our experiments were tested at a temperature (20 C) that is rather high for salmon. Basu (1959) found that the effect of carbon dioxide on active oxygen consumption rates of various fishes, including brook trout, was somewhat less at high temperatures than at lower temperatures.

#### ACKNOWLEDGMENT

The writers are grateful to Dr C. E. Warren, Professor of Fisheries, Oregon State University, for his helpful advice and support during this investigation.

#### REFERENCES

- ALABASTER, J. S., D. W. M. HERBERT, AND J. HEEMENS. 1957. The survival of rainbow trout (*Salmo gairdnerii* Richardson) and perch (*Perca fluviatilis* L.) at various concentrations of dissolved oxygen and carbon dioxide. *Ann. Appl. Biol.*, **45**(1): 177-188.
- AMERICAN PUBLIC HEALTH ASSOCIATION. 1960. Standard methods for the examination of water and wastewater. 11th ed. Am. Public Health Assoc., New York. 626 p.
- BAINBRIDGE, R. 1960. Speed and stamina in three fish. *J. Exptl. Biol.*, **37**(1): 129-153.
- BASU, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. *J. Fish. Res. Bd. Canada*, **16**(2): 175-212.
- BLACK, E. C., D. KIRKPATRICK, AND H. H. TUCKER. 1966a. Oxygen dissociation curves of the blood of brook trout (*Salvelinus fontinalis*) acclimated to summer and winter temperatures. *Ibid.*, **23**(1): 1-13.
- 1966b. Oxygen dissociation curves of the blood of landlocked salmon (*Salmo salar sebago*) acclimated to summer and winter temperatures. *Ibid.*, **23**(10): 1581-1586.

- BLACK, E. C., H. H. TUCKER, AND D. KIRKPATRICK. 1966c. Oxygen dissociation curves of the blood of Atlantic salmon (*Salmo salar*) acclimated to summer and winter temperatures. *Ibid.*, **23**(8): 1187-1195.
- 1966d. The effect of hemolysis upon the oxygen affinity of hemoglobin in the Atlantic (*Salmo salar*) and landlocked salmon (*Salmo salar sebago*). *Ibid.*, **23**(10): 1575-1580.
- BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *Ibid.*, **21**(5): 1183-1226.
- DAHLBERG, M. L. MS, 1963. Influence of dissolved oxygen and carbon dioxide on the sustained swimming speed of juvenile largemouth bass and coho salmon. M.Sc. Thesis. Oregon State University, Corvallis, Oregon.
- 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. *Trans. Am. Fish. Soc.*, **92**(2): 111-124.
- DOUDOROFF, P. 1957. Water quality requirements of fishes and effects of toxic substances. *In* M. E. Brown [ed.] *Physiology of fishes*, Vol. II. Academic Press, Inc., New York. p. 403-430.
- DOUDOROFF, P., AND M. KATZ. 1950. Critical review of literature on the toxicity of industrial wastes and their components to fish. I. Alkalies, acids, and inorganic gases. *Sewage Ind. Wastes*, **22**(11): 1432-1458.
- DOUDOROFF, P. AND C. E. WARREN. 1965. Dissolved oxygen requirements of fishes. *In* Biological problems in water pollution: Transactions of the 1962 seminar. Public Health Service Publication 999-WP-25. Robert A. Taft Sanitary Engineering Center, U.S. Public Health Service, Cincinnati, Ohio. p. 145-155.
- ELLIS, M. M. 1937. Detection and measurement of stream pollution. *U.S. Bur. Fish. Bull.* No. 22. p. 365-437.
- FERGUSON, J. K. W., AND E. C. BLACK. 1941. The transport of CO<sub>2</sub> in the blood of certain freshwater fishes. *Biol. Bull.*, **40**(2): 139-152.
- FRY, F. E. J. 1957. The aquatic respiration of fish. *In* M. E. Brown [ed.] *Physiology of fishes*, Vol. I. Academic Press, Inc., New York. p. 1-63.
- FRY, F. E. J., V. S. BLACK, AND E. C. BLACK. 1947. Influence of temperature on the asphyxiation of young goldfish (*Carassius auratus*) under various tensions of oxygen and carbon dioxide. *Biol. Bull.*, **92**(3): 217-224.
- HART, J. S. 1945. The circulation and respiratory tolerance of some Florida freshwater fishes. *Proc. Florida Acad. Sci.*, **7**: 221-246.
1957. Seasonal changes in CO<sub>2</sub> sensitivity and blood circulation in certain fresh-water fishes. *Canadian J. Zool.*, **35**: 195-200.
- KATZ, M., A. PRITCHARD, AND C. E. WARREN. 1959. Ability of some salmonids and a centrarchid to swim in water of reduced oxygen content. *Trans. Am. Fish. Soc.*, **88**: 88-95.
- MCNEIL, W. J. MS, 1956. The influence of carbon dioxide and pH on the dissolved oxygen requirements of some fresh-water fish. M.Sc. Thesis. Oregon State College, Corvallis, Oregon.
- ROOT, R. W. 1931. The respiratory function of the blood of marine fishes. *Biol. Bull.*, **61**: 427-456.
- SAUNDERS, R. L. 1962. The irrigation of the gills of fishes. II. Efficiency of oxygen uptake in relation to respiratory flow activity and concentrations of oxygen and carbon dioxide. *Canadian J. Zool.*, **40**: 817-862.
- STEWART, N. E., D. L. SHUMWAY, AND P. DOUDOROFF. 1967. The influence of oxygen concentration on the growth of juvenile largemouth bass. *J. Fish. Res. Bd. Canada*, **24**(3): 475-494.
- TITOMAS, A. E., R. E. BURROWS, AND H. H. CHENOWETH. 1964. A device for stamina measurement of fingerling salmonids. *U.S. Fish Wildlife Serv., Bur. Sport Fish. Wildlife, Res. Rept. No. 67*. 15 p.
- WINTROBE, M. M. 1961. *Clinical hematology*. 5th ed. Lea and Febiger, Philadelphia, Pa. 1186 p.