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Title: Influence of Dissolved Oxygen and Carbon Dioxide on the Sustained Swimming Speed of Juvenile Largemouth Bass and Coho Salmon

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Experiments are reported on the influence of dissolved oxygen and free carbon dioxide on the maximum sustained swimming speed of juvenile largemouth bass, Micropterus salmoides (Lacépède), and coho salmon, Oncorhynchus kisutch (Walbaum).

An apparatus in which continually renewed water of controlled temperature and dissolved gas content could be circulated through a tubular chamber at velocities up to 76 centimeters per second was employed. For each test, five fish were placed in the test chamber. After an overnight rest period during which the fish became accustomed to the chamber, the water velocity was increased to a moderate "base" velocity, and the dissolved oxygen concentration was gradually brought to the test level. The carbon dioxide concentration was adjusted either before placing the fish in the chamber or at the time of adjustment of the oxygen concentration, thus varying the duration of acclimation to elevated carbon dioxide levels. After four hours allowed for dissolved gas adjustment and training of the fish to swim at base velocity, the velocity was increased gradually, at 10-minute

intervals, until each fish had been permanently forced by the current against a screen and had been removed from the chamber. The velocity at the time of swimming failure of each fish was recorded, and when the last fish had failed, chemical analyses of the water were performed.

The swimming performance (mean swimming speed at failure) of largemouth bass at 25° C was not markedly affected by fairly high concentrations of free carbon dioxide, up to 40 mg/l at least, at any tested level of dissolved oxygen. Oxygen concentrations below about 6 mg/l impaired the swimming performance of bass. Largemouth bass swam better than coho salmon of nearly the same size at oxygen concentrations below 2.5 mg/l, but the reverse was true at higher oxygen concentrations.

Coho salmon showed a reduction in swimming speed at oxygen concentrations below about 9 mg/l when temperatures near 20° C and natural carbon dioxide concentrations near 2 mg/l were maintained. Between oxygen concentrations of about 2 mg/l and 7 or 8 mg/l, the speed decreased almost rectilinearly with decrease in the logarithm of the oxygen concentration. High concentrations of free carbon dioxide averaging 49 mg/l had more effect on the swimming speed of coho salmon at oxygen concentrations near or above the air-saturation level than at much lower concentrations; at 2 mg/l dissolved oxygen, no effect was detected. At all oxygen concentrations tested, the speeds at carbon dioxide levels near 20 mg/l differed little from speeds observed at low carbon dioxide concentrations. The slightly impaired performance of coho salmon at these moderately high carbon

dioxide levels tended to improve after overnight acclimation of the fish thereto.

The Bohr and Root effects of carbon dioxide on the oxygen transport capacity of fish blood presumably are responsible for the decrease of the swimming speed of coho salmon at high concentrations of carbon dioxide which was observed when oxygen concentrations were high. The maximum level of sustained activity at very low oxygen concentrations is believed to be determined mostly by the maximum possible rate of oxygenation of the blood at the gills, which depends on the diffusion gradient and should not be greatly influenced by carbon dioxide. The slight effect of high carbon dioxide concentrations on the performance of coho salmon at very low oxygen concentrations is thus explained.

It is concluded that free carbon dioxide probably does not materially influence the sustained swimming speed of fish in waters that are not generally unsuitable for good fish production because of excessive pollution, inasmuch as effective concentrations are not often found in such waters.

# INFLUENCE OF DISSOLVED OXYGEN AND CARBON DIOXIDE ON THE SUSTAINED SWIMMING SPEED OF JUVENILE LARGEMOUTH BASS AND COHO SALMON

by

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## INTRODUCTION

This thesis presents the results of an experimental study of the influence of dissolved oxygen and free carbon dioxide on the swimming speed of juvenile coho salmon, Oncorhynchus kisutch (Walbaum), and largemouth bass, Micropterus salmoides (Lacépède). This investigation was carried out at the Oak Creek laboratory of the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University and United States Public Health Service, located near Corvallis, Oregon. The study was performed in the spring, summer, and fall of 1962. It is one segment of a comprehensive investigation of the dissolved oxygen requirements of fish, in progress at Oregon State University. The effects of reduced oxygen concentrations, which occur often in water receiving organic wastes, on the survival, development, growth, movements, and activity of representative fishes are being investigated.

The extensive literature dealing with the influence of dissolved oxygen and carbon dioxide on the survival, oxygen consumption, and performance of fishes will not be reviewed fully. Fry (11, p. 1-55) and Doudoroff (8, p. 403-430) have briefly summarized much of the published information and cited numerous references. Doudoroff and Katz (9, p. 1445-1448) should be consulted for a critical review of early literature on the toxicity of carbon dioxide to fish. Davis et al. (7, p. 111-124) have recently reviewed and discussed the

literature pertaining to the influence of oxygen and carbon dioxide on the swimming performance of fish, including publications dealing with the active respiration of fish as influenced by these environmental factors.

The ecological importance of non-lethal variations in water quality which can influence or restrict the activity of fishes in their natural environment has been discussed by Doudoroff (8, p. 403-430). Doudoroff has pointed out that fish must be active in their natural habitat in order to find food, resist currents, reproduce, and compete effectively with other species.

In one experiment performed at 8° C, Graham (12, p. 270-288) showed that the cruising speed of speckled trout, Salvelinus fontinalis, remained constant at about 100 feet per minute down to a partial pressure of oxygen near 80 mm. Hg. (6 mg/l), below which the cruising speed declined rectilinearly with decreasing oxygen tension. Davis et al. (7, p. 111-124) found that, at various test temperatures, even slight reduction of oxygen concentration from the air-saturation levels usually resulted in some reduction of sustained swimming speeds of coho salmon and chinook salmon, Oncorhynchus tshawytscha; tested concentrations above the air-saturation levels had little or no effect on the performance of wild underyearling and hatchery-reared yearling coho salmon. The ability of juvenile coho and chinook salmon to swim for 24 to 48 hours at a moderate speed in water at 20° C with oxygen concentrations near 3 mg/l, not far above levels which are lethal for these fish, had been demonstrated earlier by Katz,

Pritchard, and Warren (14, p. 88-95).

The influence of carbon dioxide on the oxygen carrying capacity of the blood of fish and on their dissolved oxygen requirements has been studied by several authors. Black (4, p. 215-229) studied oxygen transport in the blood of four species of freshwater fish and found interspecific differences of effects of carbon dioxide. Fish blood with a high affinity for oxygen had a low sensitivity to carbon dioxide, and blood with a low affinity for oxygen had a high sensitivity to carbon dioxide. Root (19, p. 427-456) examined the blood of several marine fish and found that carbon dioxide tensions of 15 mm. Hg. prevented the saturation of the blood by oxygen even at oxygen concentrations above air-saturation. Black, Fry and Black (5, p. 412-414) sealed fish in bottles with well-oxygenated water having various concentrations of carbon dioxide and related the residual levels of dissolved oxygen at death of the fish to carbon dioxide concentrations. Results of these tests showed that when the initial dissolved oxygen tension was about 160 mm. Hg., the carbon dioxide tension at which no oxygen could be removed by the various tested fish ranged from 80 mm. Hg., for the northern blacknose shiner, Notropis heterolepis heterolepis, to 338 mm. Hg., for the northern brown bullhead, Ameiurus nebulosus nebulosus. Carbon dioxide tensions greater than about 40 mm. Hg. (113 mg/l at the lowest temperature tested) were required to affect markedly the residual dissolved oxygen level of any species. Alabaster, Herbert and Hemens (1, p. 177-188) performed experiments on the survival of rainbow trout, Salmo

gairdneri, and perch, Perca fluviatilis, at various oxygen and carbon dioxide concentrations, using aquaria and bubbling nitrogen, oxygen, and carbon dioxide through the water in suitable proportions to maintain the desired test concentrations of dissolved oxygen and free carbon dioxide. Results of tests with rainbow trout showed that, "As the carbon dioxide concentration is increased, the increase in period of survival, for a given increase of oxygen tension, is reduced" (1, p. 182). Mortalities occurred at carbon dioxide concentrations of 15 to 233 p.p.m., depending on the temperature and dissolved oxygen concentration.

There has long been evidence that fish can become fairly rapidly adapted to elevated carbon dioxide tensions (9, p. 1445). McNeil (17, p. 1-82) studied the influence of carbon dioxide and pH on the dissolved oxygen requirements of some freshwater fish, using two techniques. One of these involved placing fish in bottles that received continuous flows of water that could be treated so as to alter the dissolved gas concentrations in the bottles gradually. The other involved sealing fish in bottles with water of previously adjusted quality. Experimenting with coho salmon, he found that, "In both running-water and standing-water experiments, noticeable increases in the minimum dissolved oxygen requirements of salmon occurred at free carbon dioxide concentrations between 50 and 100 mg/l, depending on the period of acclimation and the bicarbonate alkalinity of the test water" (17, p. 74). Sealed-bottle experiments started with two different initial levels of dissolved oxygen and the same level of

carbon dioxide showed that coho salmon, when placed in bottles of water having the higher dissolved oxygen concentration, could reduce the dissolved oxygen to a lower residual level than could fish which started at the lower initial level of dissolved oxygen. This was interpreted as indicating reduction of the effectiveness of carbon dioxide due to acclimation, since the fish starting at the higher initial level of dissolved oxygen took a long time to reduce the dissolved oxygen concentration to the level at which fish exposed initially to the lower level of dissolved oxygen died.

No experiments are known to have been reported on the influence of reduced levels of dissolved oxygen together with increased levels of free carbon dioxide on the swimming performance of fish. Some work has been done on the oxygen consumption rates of active fish as affected by carbon dioxide and dissolved oxygen concentration. Basu (3, p. 175-212) measured the "active" oxygen consumption rates of five species of freshwater fish in the presence of various combinations of dissolved oxygen and carbon dioxide. A steady state of activity was maintained by a mild electric stimulus whereby the fish were made to swim in a rotating annular respirometer. Basu found that at a given level of oxygen the logarithm of the oxygen consumption rate usually decreased linearly with increasing concentration of carbon dioxide. The various dissolved oxygen levels tested gave different results. The slopes of the curves obtained at different oxygen concentrations well above and below the air-saturation values were not markedly different from those obtained at oxygen concentrations

near the air-saturation levels, except curves obtained at very low oxygen concentrations. The latter curves were much steeper, showing more marked effect of carbon dioxide on the active oxygen consumption.

One purpose of the present work was to determine what reduction, if any, of dissolved oxygen concentration below the air-saturation value had a demonstrable effect on the swimming speed of largemouth bass. Another purpose was to evaluate the degree of impairment of the swimming performance of coho salmon and largemouth bass at various concentrations of dissolved oxygen and free carbon dioxide. In each swimming performance test, five fish, confined in a tubular chamber, were subjected to controlled velocities of water with dissolved oxygen, free carbon dioxide, and temperature maintained at desired levels. After a period of time during which the fish became accustomed to the chamber, the water velocity was increased by definite increments until each fish had been permanently forced by the current against a screen at the downstream end of the chamber and had been then removed from the chamber. The velocity at the time of failure of each fish was recorded as the maximum swimming speed of the fish at the tested levels of dissolved oxygen and free carbon dioxide, this speed being only slightly higher than the maximum sustained speed.

## EXPERIMENTAL MATERIALS

Wild, juvenile largemouth bass used in these studies were seined from a small pond five miles south of Junction City, Oregon. Juvenile coho salmon were seined periodically from tributaries of the Alsea River, Benton County, and from the Yaquina River, in Lincoln County, Oregon.

All fish were graded as to size; large and small fish were discarded and only those of suitable, intermediate size were retained for use. The mean total length of the bass used was 82 millimeters; the standard deviation was 2.3 millimeters. The mean total length of the coho salmon used was 82 millimeters; the standard deviation was 4.5 millimeters.

The fish were kept in a constant temperature room at the Oak Creek laboratory in fifty-gallon glass aquaria supplied with running water from a small spring-fed stream.

The largemouth bass were held at 25° C, the test temperature, for at least 18 days before use in experiments. During the acclimation, the fish were fed an unrestricted diet of small live earthworms. 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 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 five days before use in experiments, and no more diseased fish were observed. The coho salmon were fed an unrestricted diet of tubificid worms during the holding period.

## EXPERIMENTAL APPARATUS

The experimental apparatus used in these studies was designed for subjecting fish to a rectilinear flow of water of controlled velocity, temperature, and dissolved gas content in a glass tube 60 inches long and 4 inches in diameter. Water could be circulated continually through this tubular chamber and through a heat exchanger (immersed in a cooling bath for temperature control) by means of a centrifugal pump. The pump produced, in the chamber, water velocities up to about 76 centimeters per second (2.5 feet per second), adjustable by means of a calibrated gate valve located at the pump's outlet. The water in the entire system was renewed continually at a rate of one 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 gas was used for maintaining concentrations of dissolved oxygen below air-saturation levels. Compressed air and oxygen were used for maintaining air-saturation levels of dissolved oxygen and levels above air-saturation, 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. The flows of gases through the column were controlled with two-stage pressure-reducing valves. For a detailed description of the apparatus, reference should be made

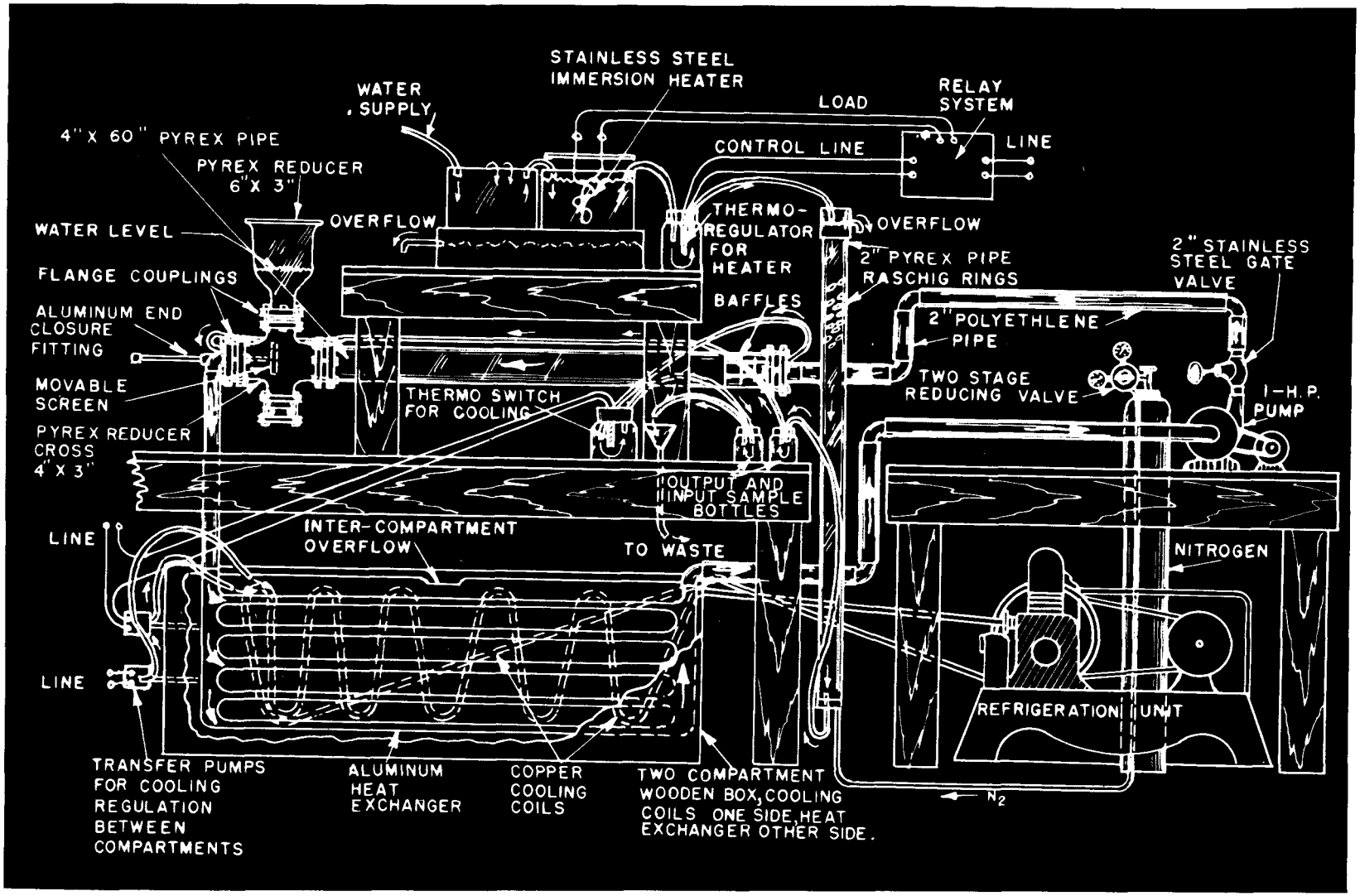


Figure 1. Semi-diagrammatic drawing of the experimental apparatus.

to Davis et al. (7, p. 111-124). Figure 1 is a schematic drawing after Katz, Pritchard, and Warren (14, p. 88-95), who first described the apparatus. Figure 2 is a photograph of the apparatus.

A few minor changes were made in the experimental apparatus shown in Figure 1 and described by Davis et al. (7, p. 113). A fixed aluminum screen was added behind the movable screen, thus enabling removal of each fish from the experimental chamber as soon as it was swept down against the movable screen at the downstream end of the chamber, without danger of the fish being swept out and through the pump. The control and measurement of the flow of exchange water through the glass column and the test chamber were facilitated by fitting a ball-displacement flowmeter and a glass stopcock into the water supply tube between the column and the chamber. This made possible more rapid adjustments of the exchange flow. All the latex rubber tubing was replaced with flexible plastic tubing (Tygon, No. R-3603). An improved temperature regulator was installed in the cooling bath, making possible more precise control of temperature in the experimental chamber. The temperature range in most experiments was less than 1.5° C, but a brief failure in the thermoregulatory system resulted in one experiment where the temperature fluctuated 3.4° C.

A graduated dial and an improved, fine-tipped indicator on the handwheel of the gate valve made it possible to adjust precisely the water velocity in the test chamber. The valve was calibrated using a small current meter (Leupold-Stevens Midget Current Meter), and a

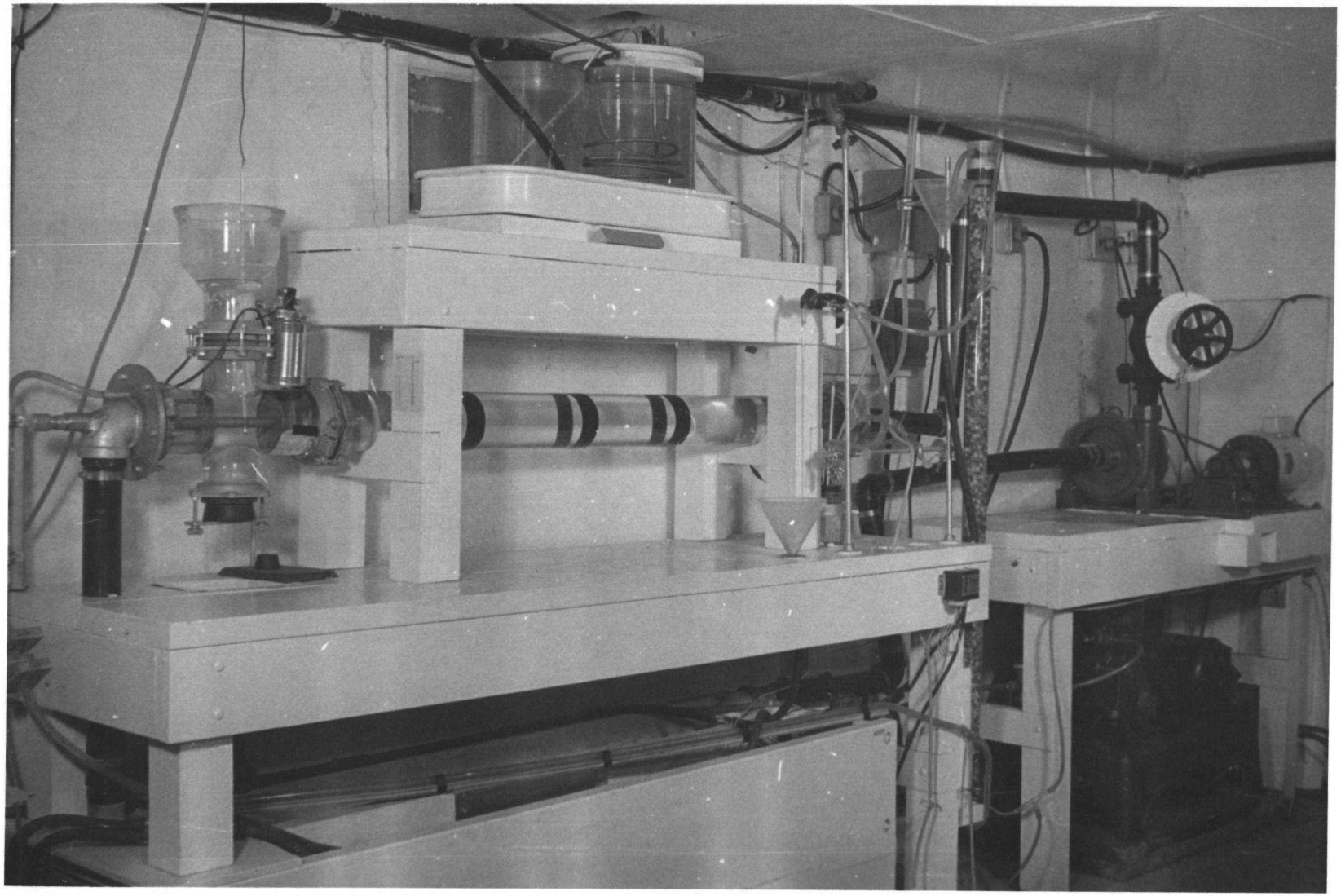

Figure 2. Photograph of the experimental apparatus.

curvilinear relationship was defined relating valve settings to water velocities. The calibration was repeated during the experiments and the relationship in question was found not to have changed materially.

## EXPERIMENTAL PROCEDURE

The procedures followed in experiments with the two species of fish were essentially the same. Five fish of uniform size were selected from the holding tank the day before a test and placed in the apparatus 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 position within the chamber with little or no exertion. The fish were left undisturbed in the apparatus until the next morning, allowing them to become accustomed to the experimental chamber. The test fish were not fed after removal from the holding tank. The following morning--about 16 hours later--the water velocity was increased by increments of 4.6 cm/sec at five-minute intervals until a velocity was reached of 15.2 cm/sec in the experiments with largemouth bass and 22.8 cm/sec in the experiments with coho salmon. These two base velocities, especially the first, are not much above the lowest velocities at which the fish must 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 four-hour period. At the end of the four-hour period, the

water velocity was increased by definite increments until all five fish failed to continue swimming. The adjustment of free carbon dioxide concentration was performed at the same time as the adjustment of the dissolved oxygen concentration in one series of tests with largemouth bass and in one series of tests with coho salmon. In all other experiments in which the fish were subjected to elevated levels of free carbon dioxide, the adjustment of carbon dioxide concentration was made 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-watt 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 possibility of premature failure of the fish due to accidental impingement on the screen thus presumably was reduced.

Both largemouth bass and coho salmon were subjected to velocity increments of 2.3 cm/sec every 10 minutes, starting in each case from the base velocity. The downstream closure was rotated as necessary in order to stimulate fish that had failed to continue swimming and had come to rest against the closure. When the failure appeared to be permanent, the water velocity at which an individual fish failed to continue swimming and was permanently forced against the movable screen was recorded. The fish was removed with the aid of a small dipnet inserted into the funnel-like receptacle at the downstream

end of the chamber; withdrawal of the movable screen permitted the current to carry the fish off the screen and into the dipnet. After removal, the fish were placed in 1-liter beakers in which they were held separately until termination of the test.

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. Dissolved oxygen concentrations near or below the air-saturation level were determined by the Alsterberg (azide) modification of the Winkler method (2, p. 309); the Pomeroy-Kirschman-Alsterberg method (2, p. 316) was used for determination of concentrations far above the air-saturation level. Carbon dioxide levels were determined by a nomographic method (2, p. 70) after first determining pH, total alkalinity (2, p. 277), temperature, and total dissolved solids (2, p. 326). After the water analyses had been completed, the fish were individually measured and weighed, and blood samples usually were taken for hemoglobin determinations.

Determinations of the hemoglobin content of the blood of coho salmon were performed in all but five tests. Hemoglobin levels were not determined in the earliest tests with largemouth bass, but were determined in all subsequent tests. The cyanmethemoglobin method, as described by Wintrobe (22, p. 381-390), was employed in all determinations. A 20-lambda sample of blood, obtained from the severed caudal artery of a fish, was diluted in five milliliters of Drabkin's solution. After converting 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 wavelength of 540 millimicrons. The optical density scale of the spectrophotometer was periodically standardized, using a hemoglobin standard, Hemotrol.

# RESULTS

## Largemouth Bass

Experiments with largemouth bass were conducted between April 25 and July 25, 1962. The test temperature was 25° C. Results of these experiments are summarized in Figures 3 and 4. Appendix Tables A and B show details of experimental conditions and descriptive data on the individual fishes.

Figure 3 shows the swimming speeds of the bass, in lengths per second, at the time of failure, plotted against oxygen concentration and grouped according to the level of free carbon dioxide and the duration of acclimation of the fish thereto. The swimming speed of each fish in lengths per second (L./sec.) was calculated by dividing the recorded speed (i.e., the water velocity at failure), in centimeters per second, by the total length of the fish in centimeters. Each point plotted in Figure 3 except one represents the mean (arithmetic) swimming speed at failure for a group of fish tested together at a particular dissolved oxygen and carbon dioxide concentration. In one test, the first failing fish was found to have an injured caudal fin, and therefore, the mean speed of the remaining four fish only was computed. The four curves shown in Figure 3 were fitted by eye to the four separately plotted sets of points obtained under different conditions with respect to carbon dioxide concentration.

One of the curves in Figure 3 represents the result of an

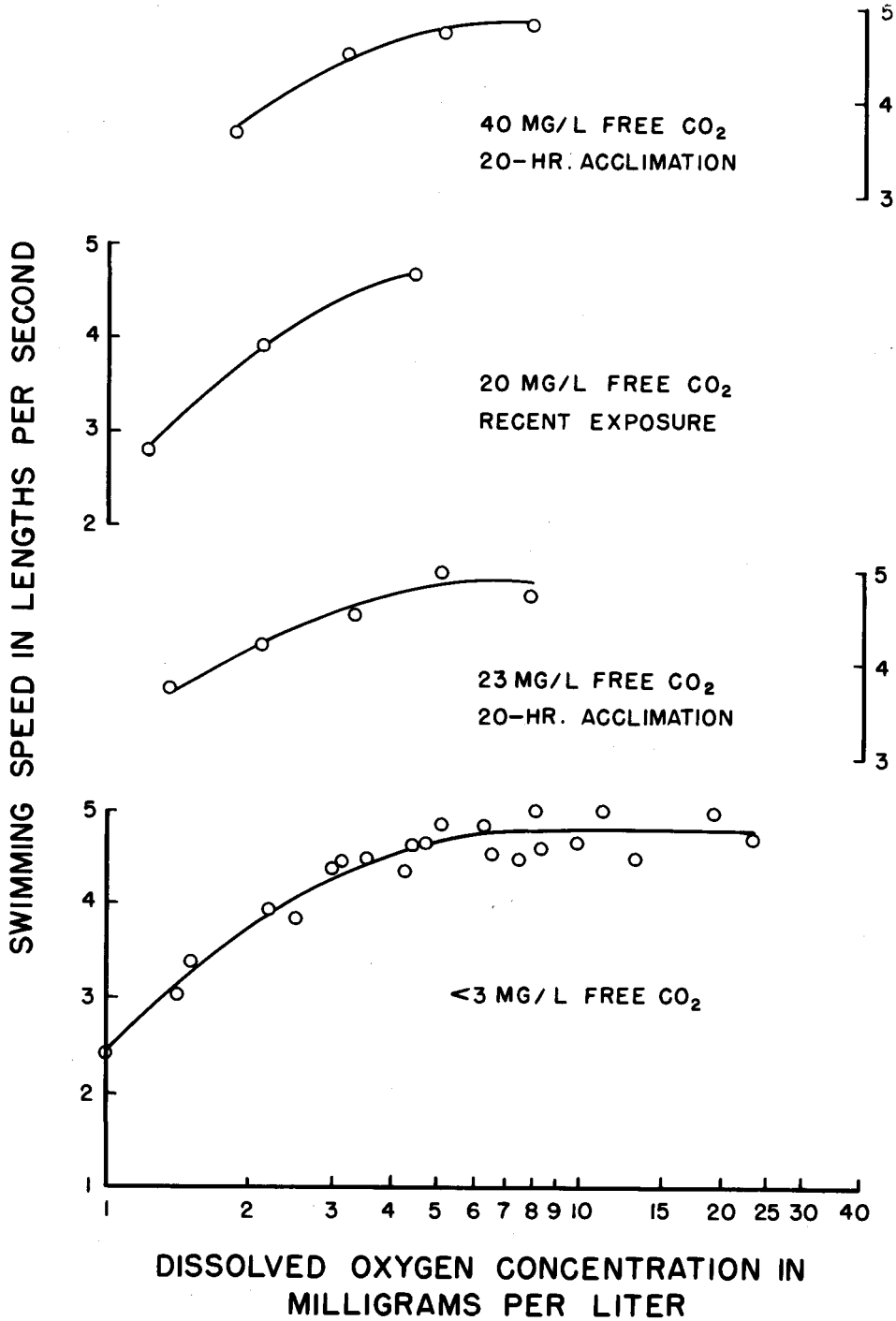


Figure 3. Swimming speeds of largemouth bass at different carbon dioxide concentrations, in relation to dissolved oxygen concentration.

experiment in which the fish had been exposed to elevated concentrations of free carbon dioxide (averaging 20 mg/l) for a short period only (i.e., recently) at the time of testing, the carbon dioxide concentration having been increased at the same time that the dissolved oxygen concentration was reduced. In the other experiments at about the same and higher carbon dioxide levels (23 and 40 mg/l), the fish had been exposed (acclimated) to these elevated levels for about 20 hours prior to the actual testing of their swimming performance.

Free carbon dioxide concentrations were not actually determined during the tests at natural, low levels of carbon dioxide on which the curve marked $<3$ mg/l free carbon dioxide is based. Determinations made under similar experimental conditions during the same season of the next year (i.e., in the spring of 1963) indicated that free carbon dioxide concentrations probably never exceeded 3 mg/l during the test period.

Figure 3 indicates that the swimming speed of largemouth bass at all carbon dioxide concentrations tested decreases gradually with a reduction in dissolved oxygen concentration below approximately 6 mg/l. Within the range of tested dissolved oxygen concentrations above 6 mg/l, variations of oxygen concentration had very little or no effect on performance.

Figure 4 facilitates comparison of the results of the four experiments depicted in Figure 3. The curve shown in Figure 4 is that which had been fitted to the data obtained at low concentrations

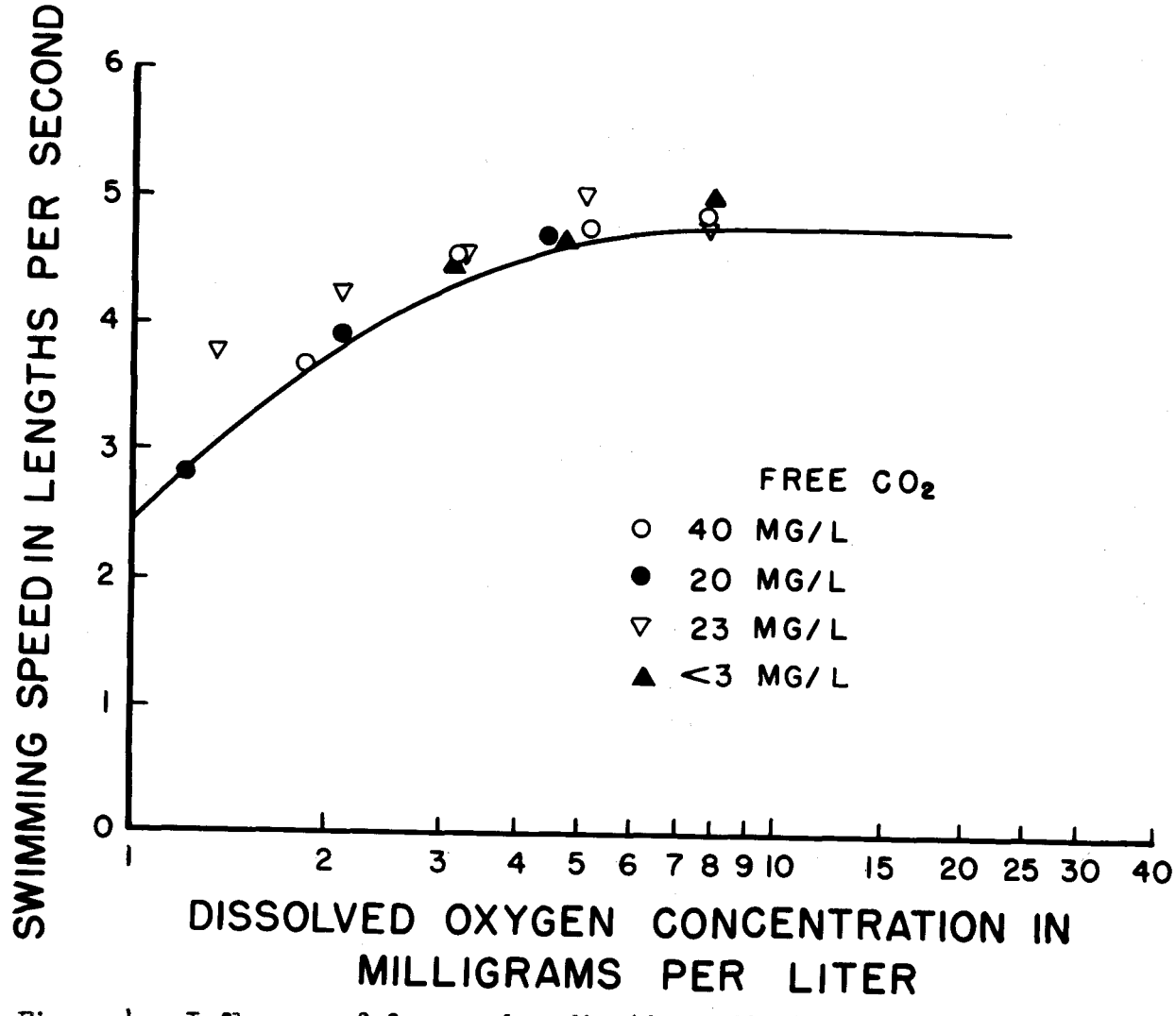


Figure 4. Influence of free carbon dioxide on the swimming speed of largemouth bass at various dissolved oxygen concentrations.

of free carbon dioxide, i.e., less than 3 mg/l (Figure 3). The data to which this curve was fitted are not shown in Figure 4, except three points (solid triangles) that represent data obtained later than the rest and at about the time when the tests at elevated carbon dioxide concentrations were performed. The individual test data from the latter experiments are all included (plotted as points, without connecting curves) in Figure 4. It can be seen that most of these data do not deviate markedly from the curve, and that those that do deviate considerably are above the curve, and not below, indicating improved swimming performance. However, since all the points found 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 equally favorable conditions. Thus, while it can be concluded that concentrations of free carbon dioxide as high as 40 mg/l or more, which are rarely found in nature, have very little or no adverse effect on the sustained swimming performance, there is not sufficient evidence of improvement of the performance at moderately elevated concentrations.

In Figure 5, the swimming speeds (i.e., water velocities) at the time of failure of the first-failing and of the third-failing largemouth bass at normal, low carbon dioxide concentrations are plotted against oxygen concentration, along with similar data from experiments with coho salmon. It can be seen that there was little difference in performance between the first-failing and third-failing fish, and

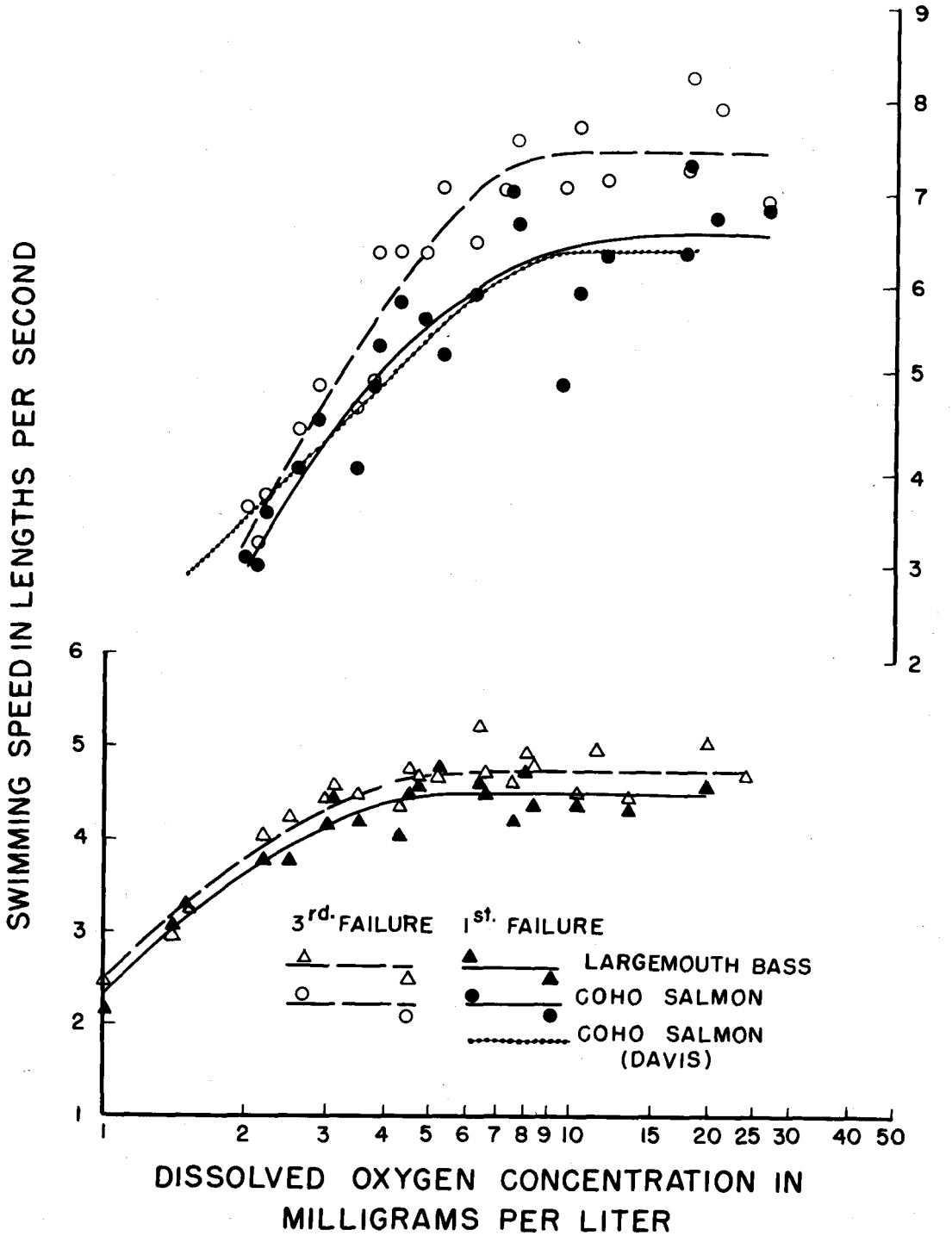


Figure 5. Swimming speeds of first-failing and third-failing coho salmon and largemouth bass at low carbon dioxide levels, in relation to dissolved oxygen concentrations.

that the data pertaining to each do not deviate widely from the respective eye-fitted curves.

Hemoglobin determinations were made on the blood of 67 juvenile largemouth bass used in the performance tests. The mean and standard deviation of the values obtained ( Appendix Table B) were 7.92 and 0.47 g/100 ml, respectively. Very little correlation (r = 0.11) was found between swimming speed and hemoglobin values. The small standard deviation indicates that the hemoglobin concentrations in the blood of the experimental animals were uniform.

Condition indices, $K_{TL}$, based on weight and total length of the fish were calculated according to the formula:

$$K_{TL} = \frac{100\ W}{L^3},$$

where W is the weight in grams and L is the total length in centimeters (15, p. 159-164). The mean and standard deviation of the condition indices obtained for largemouth bass (Appendix Table B) were 1.07 and 0.07, respectively. Early tests seemed to indicate a relationship between swimming speed and condition index; however, the product-moment correlation proved low (r = 0.06, N = 164) after all experiments had been completed.

Coho Salmon

Experiments with coho salmon were conducted between August 6 and November 9, 1962. The test temperature was 20° C. Results of these experiments are summarized in Figures 6 and 7. Appendix tables C and

D give details of experimental conditions and descriptive data on the individual fish.

Figure 6 shows the swimming speeds of the salmon, in lengths per second, at the time of their failure, plotted against oxygen concentration. Again the data are grouped according to the free carbon dioxide concentrations and the duration of exposure thereto. Curves were fitted by eye to the points representing the mean (arithmetic) sustained swimming speeds of groups of fish tested at different dissolved oxygen concentrations at each of three widely different carbon dioxide levels. As in the experiments with largemouth bass, tests at carbon dioxide concentrations near 20 mg/l were performed both with and without prior overnight acclimation of the salmon (for about 20 hours) to the increased carbon dioxide concentration.

Five fish were used in each test and the water velocity at failure was recorded for each of the five fish except in three tests where only four terminal velocities were recorded and one test where three terminal velocities were noted. In each of these tests, at least one fish (two in the last-mentioned test only) stayed in a favorable position near the baffles at the upstream end of the test chamber and thus was seemingly able to withstand water velocities much higher than the terminal velocities recorded for other fish tested. In other experiments the fish did not find the favorable positions described, and all five terminal velocities were used in computing the mean. Davis et al. (7, p. 115) found fish deriving advantage from the eddies behind the baffles often when using chinook

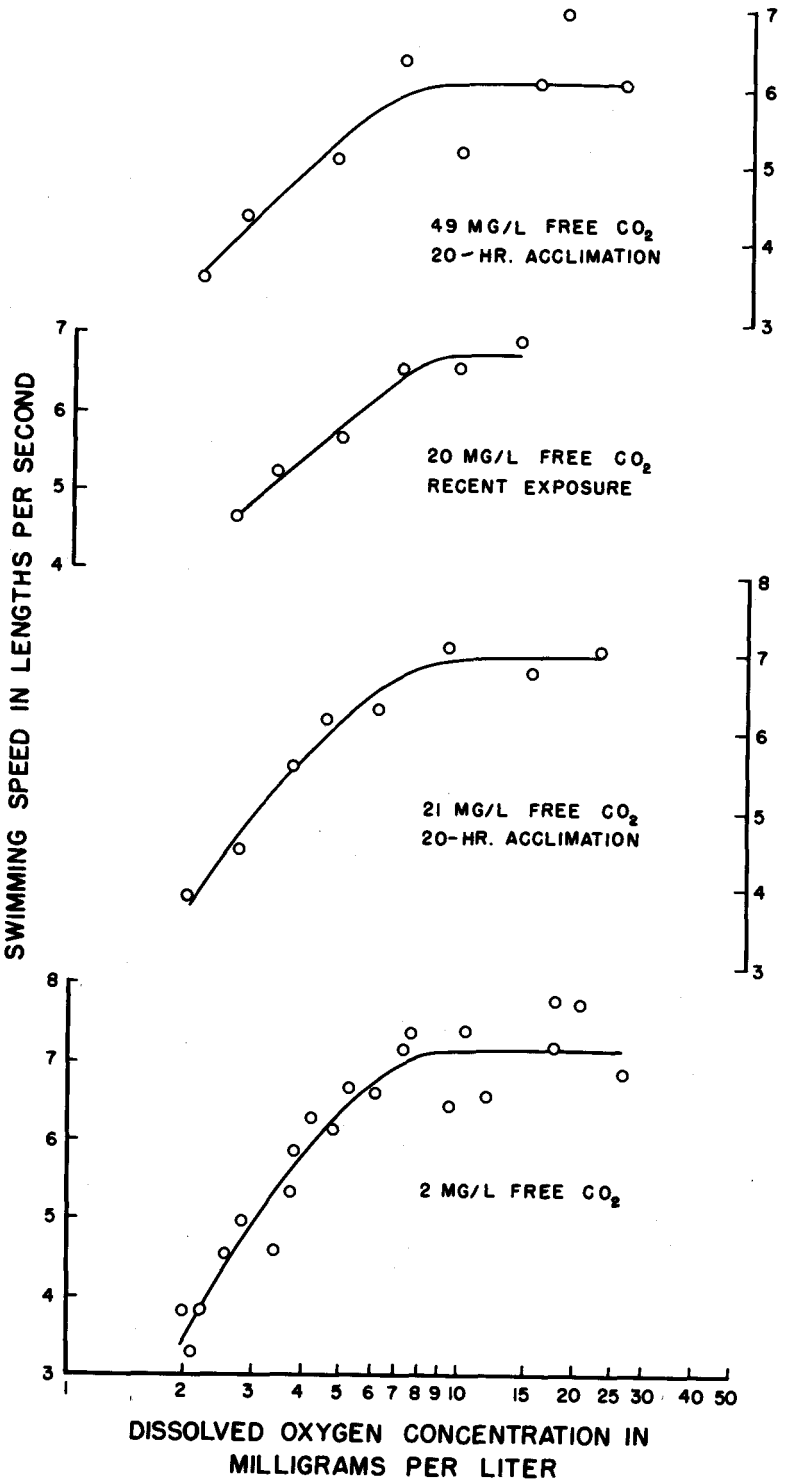


Figure 6. Swimming speeds of coho salmon at different carbon dioxide concentrations, in relation to dissolved oxygen concentration.

salmon in the same experimental apparatus, but only rarely when using coho salmon.

Figure 6 shows that the swimming speeds of coho salmon decreased with reduction in dissolved oxygen concentration below about 9 mg/l. Within the range of tested dissolved oxygen concentrations above 9 mg/l, variation of oxygen concentration had only little or no effect on performance.

Figure 7 facilitates comparison of the curves shown in Figure 6. Elevated carbon dioxide concentrations near 20 mg/l can be seen to have little effect on the maximum sustained swimming speeds of coho salmon, especially when the fish have become adjusted thereto. Even after overnight acclimation, free carbon dioxide concentrations near 49 mg/l seem to have had a pronounced effect on the swimming speed, but only at dissolved oxygen concentrations above 2 mg/l. At the 2 mg/l level of dissolved oxygen, the effect of the high free carbon dioxide concentration is negligible, and the greatest effect is seen at oxygen concentrations near and above the air-saturation level.

Condition indices, $K_{FL}$, based on the weights of the fish in grams and fork lengths in centimeters, were calculated using the same formula as that used in computing condition indices of bass, except that fork length was substituted for total length in the formula. These condition indices were calculated for 214 coho salmon (Appendix Table D). The mean and the standard deviation were found to be 1.04 and 0.07, respectively. Calculation of the product-moment correlation coefficient ($r = 0.06$) indicated that relationship between condition

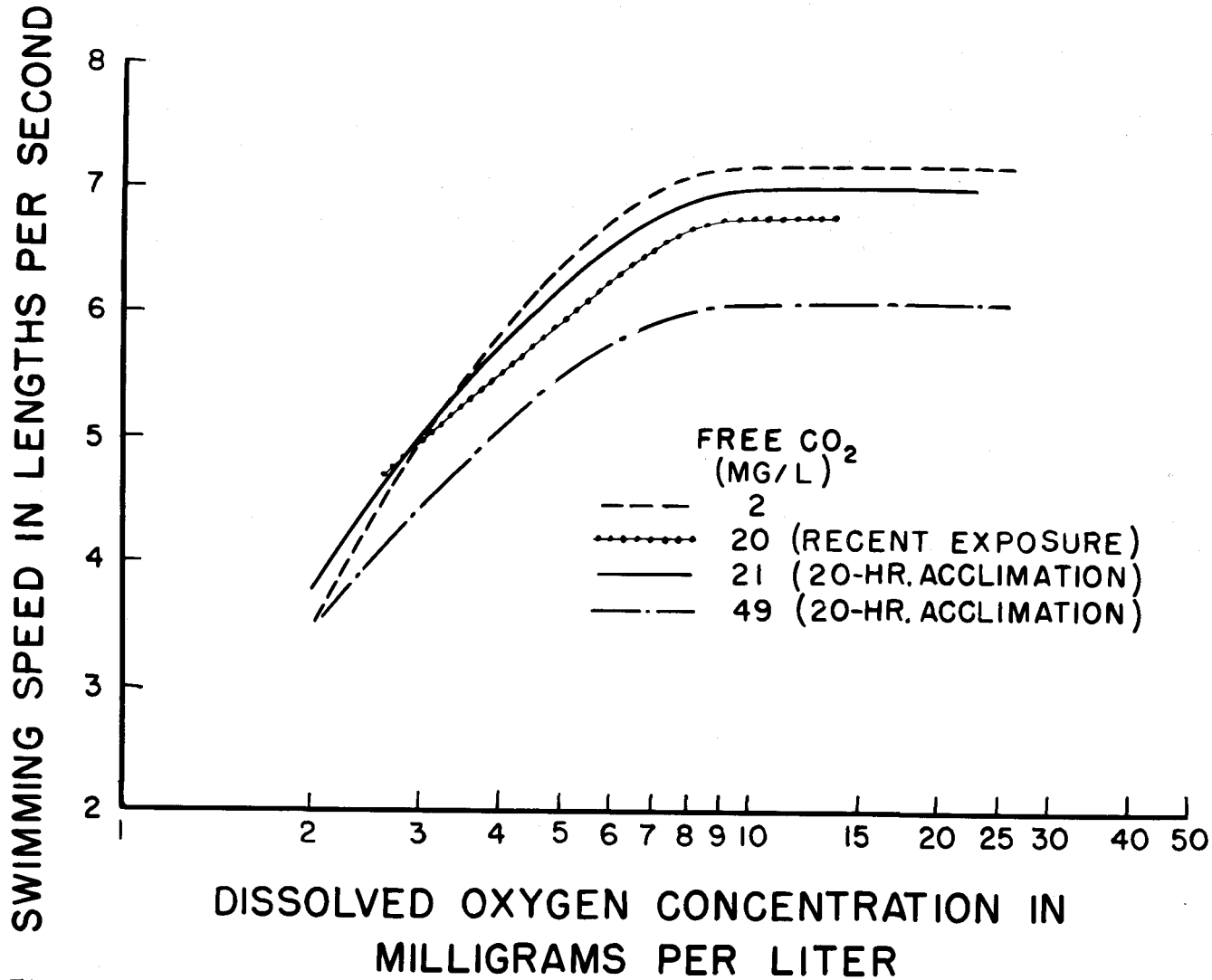


Figure 7. Comparison of curves relating swimming speeds of coho salmon to dissolved oxygen concentration at different levels of free carbon dioxide.

factor and swimming speed was nonexistent.

Hemoglobin determinations were made on the blood of 184 coho salmon during the investigation (Appendix Table D). The mean value and the standard deviation were found to be 6.85 and 0.82 g/100 ml, respectively. Very little relationship between hemoglobin values and swimming speed is indicated by the low product-moment correlation coefficient ($r = 0.12$).

Statistical analyses of the curves shown in Figures 6 and 7 were performed in order to test the significance of the observed differences in swimming speeds of the coho salmon at various levels of free carbon dioxide. The curves were divided into two separate phases for analyses. The flat (horizontal) portions of the curves, where dissolved oxygen concentration did not influence swimming performance, were compared using a t-test for difference between sample means (16, p. 131). Comparisons were made between the experiment performed at the free carbon dioxide concentrations of 21 mg/l (with 20-hour acclimation) and each of the other three experiments, and also between the experiments at the lowest and highest carbon dioxide concentrations tested (2 mg/l and 49 mg/l). The only difference in swimming speeds that was found to be significant at the 1 percent level ($t_{11} = 2.87$) in thus comparing the flat portions of the curves was the difference between the fish tested at the lowest and the highest carbon dioxide concentrations. However, there is a difference significant at the 10 percent level ($t_5 = 1.75$) between the swimming speeds observed at free carbon dioxide concentrations of 21 mg/l and 49 mg/l after

20-hour acclimation to each.

Assuming a linear relationship in the sloping portion of each curve, least-squares estimates were calculated for each experiment from the equation:

$$Y_i = A + B \log X$$

where $Y_i$ is the mean swimming speed in lengths per second, A is the Y-axis intercept, B is the regression coefficient, and log X is the logarithm of the dissolved oxygen concentration at the observed $Y_i$. Generally, with data of this type, there are several hypotheses of interest which may be tested by covariance analyses. The first hypothesis to be tested is whether all data under consideration can be properly described by one regression line. For the data along the sloping portions of all the curves, this hypothesis was accepted ($F_{6,17} = 2.5479$, $p = 0.01$), and no further hypotheses were tested.

The reason why a significant difference is demonstrable between the flat portions of some of the curves and not between the sloping portions will be considered in the Discussion section.

In Figure 5, the swimming speeds at failure of the first-failing and third-failing coho salmon tested at low carbon dioxide concentrations (<3 mg/l) are plotted against oxygen concentration. Curves were fitted by eye to each set of experimental data. A curve relating the swimming speeds of first-failing coho salmon to oxygen concentration, fitted to the data of Davis et al. (7, p. 116), which were obtained at the same test temperature, is included for comparative purposes. The individual data of Davis et al. are not shown.

A marked difference can be seen between the swimming speeds of first-failing and third-failing coho salmon. First-failing fish exhibit variation in swimming performance wider at all levels of dissolved oxygen than that shown by third-failing fish. There seems to be very little difference between the curves based on first-failure data reported here and the first-failure data reported by Davis et al. (7, p. 116), whose under-yearling coho salmon were of about the same size as those used in the present study. The small difference between the lower portions of these curves may be disregarded, because that of the curve fitted to the data of Davis et al. is based on a single observation of a failure that occurred at the base velocity. Davis et al. (7, p. 117) believe that points based on failures observed at the base velocity may not be completely valid.

# DISCUSSION

It has been shown that the maximum sustained swimming speed of largemouth bass at 25° C is not markedly affected by fairly high concentrations of free carbon dioxide, up to 40 mg/l at least, at any tested level of dissolved oxygen. Dissolved oxygen concentrations below about 6 mg/l impaired the swimming performance of the bass. Coho salmon showed a reduction in swimming speed at dissolved oxygen concentrations below about 9 mg/l when temperatures near 20° C and natural concentrations of free carbon dioxide near 2 mg/l were maintained. Between dissolved oxygen concentrations of about 2 mg/l and 7 or 8 mg/l, the speed decreased almost rectilinearly with decrease in the logarithm of the dissolved oxygen concentration. High concentrations of free carbon dioxide averaging 49 mg/l seemed to have a more pronounced effect on the swimming speed of coho salmon at dissolved oxygen concentrations near or above the air-saturation value than at dissolved oxygen concentrations far below air-saturation. This apparent difference in the effectiveness of carbon dioxide at different dissolved oxygen levels may be considered in the light of available information concerning the influence of the gas on the transport of oxygen by fish blood.

The effect of free carbon dioxide on the oxygen transport capacity of the blood of fish has been studied extensively. Root (19, p. 427-456), Black (4, p. 215-229), Black and Irving (6, p. 357), Root and Irving (20, p. 307-323; 21, p. 207-212), and Prosser and

Brown (18, p. 217-219) have summarized the literature. Although fish blood has been studied extensively, only one reference was found pertaining to salmonids (4, p. 222). One of the characteristics of fish blood is that at high concentrations of carbon dioxide the hemoglobin never becomes completely saturated with oxygen, even when partial pressures of oxygen are extremely high (11, p. 18). The observations of Ferguson and Black on the blood of rainbow trout, reported by Black (4, p. 222), showed that "in the presence of $CO_2$ even a pressure of 700 mm. oxygen failed to restore the amount of oxygen combined with the hemoglobin to its former value." This effect was first noted by Root (19, p. 427-456) in several species of marine fish, and is often called the Root effect. Another influence of carbon dioxide on the blood of fish is the well-known Bohr effect (18, p. 217). As the partial pressure of carbon dioxide increases, a higher oxygen tension is required for the loading of blood with oxygen, and the unloading tension is correspondingly increased. The Bohr effect is thought to be of advantage to fish, as it promotes discharge of oxygen from the blood to the tissues. The Bohr and Root effects of carbon dioxide on the blood would seem to explain why the swimming speed of coho salmon decreased at high free carbon dioxide concentrations when dissolved oxygen concentrations were near or above air-saturation. Since the oxygen requirement of the tissues increases with increasing activity, the intensity of sustained activity may, under some conditions, be limited by the capacity of the blood to transport oxygen to the tissues. Whether the sustained

swimming speed of healthy (not anemic) salmon at high dissolved oxygen and normal carbon dioxide concentrations is or is not limited by the oxygen transport capacity of the blood is uncertain. This question has been discussed by Davis et al. (7, p. 122), who consider also the factors that may limit sustained swimming speeds at reduced oxygen concentrations. In any event, it seems safe to assume that the speed at any given high oxygen tension in the ambient medium can be limited by sufficiently severe reduction of the oxygen carrying capacity of the blood at that oxygen tension, due to carbon dioxide and its Root and Bohr effects, or to anemia, as suggested by Davis et al.

As the concentration of dissolved oxygen in the water is decreased, the pressure gradient existing between the oxygen of the venous blood and the water bathing the gills also decreases. The extraction of sufficient oxygen from water with decreasing dissolved oxygen concentration can be maintained up to a point by passing more water over the gills. Finally, a point is reached where irrigation of the gill surfaces cannot be further increased to supply enough oxygen for nearly complete oxygenation of the blood of active fish, and the activity must be decreased. Consequently, it appears that the oxygen transport capacity of the blood and the influence on it of carbon dioxide should become less important, and the maximum possible rate of oxygenation of the blood at the gills should largely determine the maximum level of sustained activity at very low oxygen concentrations.

The relative importance of the above-mentioned two factors that

may limit the sustained swimming speed of coho salmon, namely, the oxygen capacity of their blood and the maximum rate of oxygenation of the blood at the gills (which is dependent on the diffusion gradient) clearly must be different at different oxygen concentrations. The first must be more important at very high oxygen concentrations, and the second at low concentrations. The oxygen transport capacity of the blood is directly affected by high concentrations of carbon dioxide, whereas the rate of oxygenation of the blood at the gills at low oxygen concentrations can be only indirectly and slightly affected, it would seem, if it is affected at all. It is reasonable to expect some gradation of the influence of carbon dioxide on the swimming speed as the oxygen concentration is reduced, especially in view of the fact that the Bohr effect is generally more pronounced at oxygen tensions well below the atmospheric tension than at higher tensions. This gradation is seen in Figure 6, where the curves relating swimming speed to oxygen concentration at the lowest and highest tested carbon dioxide concentrations approach a common point as the oxygen concentration decreases to the lowest tested level.

The results reported here, indicating that high free carbon dioxide concentrations have much less effect on the swimming performance of coho salmon at very low dissolved oxygen concentrations than at high concentrations, seem to be seriously in conflict with the results of some experiments on active oxygen consumption rates of fish reported by Basu (3, p. 187-190). Basu's data show that free carbon dioxide has a considerably greater effect on the active rates

of oxygen consumption of some fish at very low dissolved oxygen concentrations than at higher concentrations. The effects of carbon dioxide on the active oxygen consumption rates of speckled trout at different oxygen concentrations equal to and above 44 percent air-saturation did not differ markedly. Experiments with speckled trout were not performed at dissolved oxygen levels below 44 percent air-saturation. Comparison of the results of experiments reported here with those of Basu's experiments is difficult, because of the difference of species of fish used and of test temperatures, and because Basu measured oxygen consumption, not swimming speed. Nevertheless, the apparent lack of agreement between Basu's results and those reported here is noteworthy and somewhat surprising, inasmuch as the sustained swimming speed of fish and their active or maximum oxygen uptake rate are generally assumed to be closely related and to be similarly limited by environmental factors. The swimming performance has been considered to be a function of "scope for activity", the difference between the active and standard oxygen uptake rates (11, p. 51). In view of considerations presented above, it is difficult to understand why the active oxygen uptake rates of all fish tested by Basu at very low oxygen concentrations were more severely affected by carbon dioxide at these low oxygen concentrations than at higher dissolved oxygen levels.

Basu (3, p. 185) showed an increased effect of carbon dioxide on the active oxygen consumption rate of fish at reduced temperatures. Coho salmon in experiments reported here were subjected to a

temperature that is rather high for salmon (20° C), and a greater effect of carbon dioxide on their performance might have been observed had the test temperature been lower.

There is evidence that acclimation modifies the influence of free carbon dioxide on the swimming performance of coho salmon. The results of tests at nearly the same, moderately high level of free carbon dioxide (about 20 mg/l), performed after different periods of exposure of the fish to this level, indicate that swimming performance tended to improve with increasing exposure or acclimation time (Figure 7). In both series of tests under comparison, the fish had been exposed to the elevated carbon dioxide concentration for some time before their performance was measured, and, perhaps for this reason, the difference of the results obtained was not statistically significant. However, this apparent difference is in agreement with the results of McNeil's (17, p. 1-82) experiments on the resistance of resting coho salmon to low oxygen and high free carbon dioxide concentrations. McNeil noted that, even though the results of the two kinds of experiments performed by him are not entirely comparable, a general comparison was justified, because the difference in results suggested that acclimation to carbon dioxide is important. McNeil (17, p. 64) states:

> At dissolved oxygen concentrations near 6 mg/l salmon which had no opportunity to become acclimatized to test concentrations of carbon dioxide (standing-water tests) died in the presence of about two-thirds of the content of carbon dioxide required to kill fish that had the opportunity to acclimatize themselves over a six-hour period (running-water tests). When the initial dissolved

> oxygen content in the standing-water tests was reduced from 6 mg/l to 3 mg/l, the unacclimatized fish died at once at this dissolved oxygen concentration in the presence of carbon dioxide concentrations approximating one-half of the concentration required to cause death of fish at the same dissolved oxygen value in the running-water tests.

The above observations suggest that effects on fish of moderate concentrations of free carbon dioxide that have been reported in the literature, such as the effects on active oxygen uptake rates described by Basu and the effects on tolerance of low oxygen concentrations reported by Alabaster, Herbert, and Hemens (1, p. 177-188), are transient effects that cannot be often very important under natural conditions.

The finding that the swimming speed of largemouth bass was not markedly affected by the levels of carbon dioxide tested is not very surprising, in view of their tolerance of very high concentrations of the gas. Hart (13, p. 226) found that largemouth bass were unable to remove oxygen from water one-half saturated with dissolved atmospheric oxygen only when the carbon dioxide concentration was 175 mg/l or more.

The curves in Figure 5 relating the swimming speeds of first-failing and third-failing bass at low carbon dioxide concentrations to the concentration of dissolved oxygen are generally similar in shape to the corresponding curves for coho salmon shown in the same figure, but the performance of the bass is clearly seen to be much less affected than that of coho salmon by reduced levels of dissolved oxygen. The swimming speed of largemouth bass at high oxygen

concentrations is less than that of coho salmon of about the same size. However, it does not decrease appreciably until the dissolved oxygen concentration is reduced below 5 or 6 mg/l, whereas the swimming speed of coho salmon is appreciably reduced at dissolved oxygen concentrations not far below 9 mg/l, and decreases more sharply than that of the bass with further reduction of oxygen concentration. Thus, if the curves for largemouth bass in Figure 5 were superimposed on the corresponding curves for coho salmon, they would intersect, showing the bass to be better swimmers than coho salmon at dissolved oxygen concentrations below 2.5 mg/l. Figure 5 shows that the median swimming speed at failure of coho salmon at the dissolved oxygen concentration of 3 mg/l is less than the corresponding speed at the air-saturation level of dissolved oxygen by about 35 percent, whereas the speed of largemouth bass at the 3 mg/l level is less than the speed at the air-saturation level of dissolved oxygen by only about 9 percent. Reduction of the sustained swimming speed of largemouth bass (median speed at failure) by 35 percent, from the speed at the air-saturation level of dissolved oxygen, can be seen to occur at an oxygen concentration near 1.3 mg/l.

In natural and polluted stream waters that are not almost entirely devoid of dissolved oxygen, concentrations of free carbon dioxide are not likely often to approach those that have been tested in the course of this study. Ellis (10, p. 388-391) determined free carbon dioxide concentrations in various American rivers and found that they generally did not exceed 14 mg/l in polluted as well as

unpolluted river waters. Alabaster, Herbert, and Hemens (2, p. 187) noted that "Carbon dioxide concentrations up to 50 p.p.m. have been observed in a (British) stream containing sewage effluent." Not only are such high concentrations of free carbon dioxide undoubtedly rare in fish habitats, but they also are not likely to occur suddenly or to persist for very long periods in waters that are otherwise suitable for valuable fish populations. It can be concluded that free carbon dioxide probably does not materially influence the sustained swimming speed of fish in waters that are not generally unsuitable for good fish production because of excessive pollution.

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# APPENDIX

Table A. Conditions of experiments with largemouth bass

| Exper. Number | Date 1962 | Temperature (C°) Mean | Range | Diss. Oxygen (mg/l) | Free $CO_2$ (mg/l) | pH | Total Alkalinity (mg/l)* |
|---|---|---|---|---|---|---|---|
| 1 | 4/25 | 24.7 | 23.9-25.7 | 8.40 | -- | -- | -- |
| 2 | 4/26 | 25.1 | 24.8-25.4 | 5.20 | -- | -- | -- |
| 3 | 4/27 | 25.2 | 24.9-25.5 | 2.20 | -- | -- | -- |
| 4 | 4/28 | 25.1 | 24.8-25.4 | 6.40 | -- | -- | -- |
| 5 | 4/29 | 24.8 | 24.2-25.6 | 13.30 | -- | -- | -- |
| 6 | 4/30 | 25.2 | 24.4-28.0 | 1.40 | -- | -- | -- |
| 7 | 5/1 | 25.1 | 24.4-25.9 | 3.50 | -- | -- | -- |
| 8 | 5/5 | 24.9 | 24.0-25.5 | 11.40 | -- | -- | -- |
| 9 | 5/8 | 25.1 | 24.2-25.5 | 1.00 | -- | -- | -- |
| 10 | 5/9 | 25.0 | 24.8-25.5 | 19.70 | -- | -- | -- |
| 11 | 5/10 | 24.9 | 24.4-25.6 | 4.50 | -- | -- | -- |
| 12 | 5/11 | 24.9 | 24.0-25.5 | 3.00 | -- | -- | -- |
| 13 | 5/14 | 24.9 | 23.4-25.5 | 10.30 | -- | -- | -- |
| 14 | 5/15 | 25.2 | 24.9-25.7 | 4.30 | -- | -- | -- |
| 15 | 5/16 | 25.1 | 24.9-25.3 | 2.50 | -- | -- | -- |
| 16 | 5/17 | 24.9 | 24.2-25.4 | 6.60 | -- | -- | -- |
| 17 | 5/18 | 24.8 | 24.5-25.2 | 1.50 | -- | -- | -- |
| 18 | 5/23 | 25.0 | 24.7-25.5 | 24.00 | -- | -- | -- |
| 19 | 5/24 | 25.1 | 24.1-25.2 | 7.60 | -- | -- | -- |
| 20 | 7/4 | 25.1 | 25.1-25.2 | 4.70 | -- | -- | -- |
| 21 | 6/26 | 24.7 | 24.3-25.4 | 8.10 | 3.0 | 7.8 | 85 |
| 22 | 7/5 | 25.0 | 24.5-25.8 | 3.10 | -- | -- | -- |
| 23 | 7/10 | 25.0 | 24.4-25.3 | 7.90 | 22 | 6.85 | 94 |
| 24 | 7/11 | 24.9 | 24.5-25.8 | 3.30 | 27 | 6.65 | 92 |
| 25 | 7/12 | 25.3 | 25.1-25.3 | 2.10 | 21 | 6.85 | |
| 26 | 7/13 | 24.9 | 24.6-25.5 | 1.35 | 24 | 6.80 | 94 |
| 27 | 7/16 | 24.9 | 24.5-25.6 | 5.10 | 24 | 6.80 | 96 |
| 28 | 7/17 | 23.2 | 22.2-24.6 | 1.85 | 38 | 6.60 | |
| 29 | 7/18 | 24.2 | 24.0-25.5 | 7.85 | 38 | 6.60 | 96 |
| 30 | 7/19 | 24.8 | 23.8-25.4 | 3.20 | 43 | 6.55 | |
| 31 | 7/20 | 24.8 | 23.8-25.8 | 5.10 | 48 | 6.50 | |
| 32 | 7/25 | 25.0 | 24.8-25.3 | 2.10 | 15 | 7.00 | |
| 33 | 7/25 | 23.8 | 23.0-25.3 | 1.20 | 19 | 6.90 | 97 |

* Bicarbonate alkalinity expressed as the calcium carbonate ($CaCO_3$ equivalent. Total dissolved solids ranged between 130 and 167 mg/l.

Table B. Descriptive data on individual largemouth bass and their maximum swimming speeds at which failure occurred (in centimeters per second and lengths per second). Fish are numbered in the order of their failure in each experiment.

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 1 | | | | | | |
| 1 | 82 | 4.66 | 0.84 | -- | 35.8 | 4.36 |
| 2 | 81 | 4.95 | 0.93 | -- | 35.8 | 4.41 |
| 3 | 75 | 4.00 | 0.95 | -- | 35.8 | 4.77 |
| 4 | 83 | 4.95 | 0.86 | -- | 35.8 | 4.31 |
| 5 | 83 | 5.73 | 1.00 | -- | 42.7 | 5.14 |
| Exper. 2 | | | | | | |
| 1 | 75 | 4.01 | 0.95 | -- | 35.8 | 4.77 |
| 2 | 76 | 4.28 | 0.97 | -- | 35.8 | 4.71 |
| 3 | 87 | 6.97 | 1.06 | -- | 40.4 | 4.64 |
| 4 | 88 | 6.63 | 0.97 | -- | 42.7 | 4.85 |
| 5 | 83 | 5.73 | 1.00 | -- | 45.0 | 5.42 |
| Exper. 3 | | | | | | |
| 1 | 83 | 6.02 | 1.05 | -- | 31.2 | 3.75 |
| 2 | 82 | 5.40 | 0.98 | -- | 31.2 | 3.80 |
| 3 | 83 | 5.94 | 1.04 | -- | 33.5 | 4.03 |
| 4 | 85 | 6.38 | 1.04 | -- | 33.5 | 3.94 |
| 5 | 82 | 6.44 | 1.17 | -- | 35.8 | 4.36 |
| Exper. 4 | | | | | | |
| 1 | 83 | 5.80 | 1.01 | -- | 38.1 | 4.59 |
| 2 | 87 | 6.62 | 1.00 | -- | 40.4 | 4.64 |
| 3 | 82 | 5.57 | 1.01 | -- | 42.7 | 5.20 |
| 4 | 84 | 6.20 | 1.05 | -- | 42.7 | 5.08 |
| 5 | 87 | 6.82 | 1.04 | -- | 42.7 | 4.90 |
| Exper. 5 | | | | | | |
| 1 | 83 | 5.58 | 0.98 | -- | 35.8 | 4.31 |
| 2 | 82 | 5.23 | 0.95 | -- | 35.8 | 4.36 |
| 3 | 81 | 4.60 | 0.86 | -- | 35.8 | 4.41 |
| 4 | 87 | 5.72 | 0.87 | -- | 40.4 | 4.64 |
| 5 | 87 | 6.59 | 1.00 | -- | 42.7 | 4.90 |
| Exper. 6 | | | | | | |
| 1 | 80 | 5.33 | 1.04 | -- | 24.4 | 3.05 |
| 2 | 80 | 5.05 | 0.99 | -- | 24.4 | 3.05 |
| 3 | 83 | 5.22 | 0.91 | -- | 24.4 | 2.93 |
| 4 | 80 | 5.10 | 1.00 | -- | 26.7 | 3.33 |
| 5 | 83 | 5.50 | 0.96 | -- | 26.7 | 3.21 |

Table B, Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 7 | | | | | | |
| 1 | 80 | 5.10 | 1.00 | -- | 33.5 | 4.18 |
| 2 | 80 | 5.06 | 0.99 | -- | 35.8 | 4.47 |
| 3 | 80 | 4.99 | 0.97 | -- | 35.8 | 4.47 |
| 4 | 80 | 5.67 | 1.10 | -- | 38.1 | 4.76 |
| 5 | 82 | 5.71 | 1.04 | -- | 38.1 | 4.64 |
| Exper. 8 | | | | | | |
| 1 | 81 | 5.55 | 1.04 | -- | 40.4 | 4.98 |
| 2 | 83 | 6.00 | 1.05 | -- | 40.4 | 4.86 |
| 3 | 82 | 6.18 | 1.11 | -- | 40.4 | 4.92 |
| 4 | 83 | 6.42 | 1.12 | -- | 42.7 | 5.14 |
| 5 | 83 | 6.37 | 1.11 | -- | 42.7 | 5.14 |
| Exper. 9 | | | | | | |
| 1 | 82 | 6.19 | 1.12 | -- | 17.5 | 2.13 |
| 2 | 82 | 5.40 | 0.98 | -- | 19.8 | 2.41 |
| 3 | 81 | 5.51 | 1.03 | -- | 19.8 | 2.44 |
| 4 | 85 | 6.86 | 1.12 | -- | 19.8 | 2.32 |
| 5 | 80 | 5.80 | 1.13 | -- | 22.1 | 2.76 |
| Exper. 10 | | | | | | |
| 1 | 83 | 5.73 | 1.00 | -- | 38.1 | 4.59 |
| 2 | 81 | 5.52 | 1.04 | -- | 40.4 | 4.98 |
| 3 | 80 | 5.78 | 1.13 | -- | 40.4 | 5.05 |
| 4 | 81 | 5.59 | 1.05 | -- | 40.4 | 4.98 |
| 5 | 83 | 6.30 | 1.10 | -- | 42.7 | 5.14 |
| Exper. 11 | | | | | | |
| 1 | 80 | 5.20 | 1.02 | -- | 35.8 | 4.47 |
| 2 | 82 | 5.97 | 1.08 | -- | 38.1 | 4.64 |
| 3 | 80 | 5.45 | 1.06 | -- | 38.1 | 4.76 |
| 4 | 81 | 5.88 | 1.11 | -- | 38.1 | 4.70 |
| 5 | 81 | 5.94 | 1.12 | -- | 38.1 | 4.70 |
| Exper. 12 | | | | | | |
| 1 | 81 | 4.66 | 0.88 | -- | 33.5 | 4.13 |
| 2 | 81 | 5.90 | 1.11 | -- | 35.8 | 4.41 |
| 3 | 81 | 5.85 | 1.10 | -- | 35.8 | 4.41 |
| 4 | 83 | 6.25 | 1.09 | -- | 35.8 | 4.31 |
| 5 | 81 | 5.72 | 1.08 | -- | 38.1 | 4.70 |
| Exper. 13 | | | | | | |
| 1 | 82 | 5.80 | 1.05 | -- | 35.8 | 4.36 |
| 2 | 81 | 5.65 | 1.06 | -- | 38.1 | 4.70 |
| 3 | 85 | 6.45 | 1.05 | -- | 38.1 | 4.48 |
| 4 | 83 | 6.33 | 1.11 | -- | 38.1 | 4.59 |
| 5 | 83 | 5.92 | 1.04 | -- | 42.7 | 5.14 |

Table B. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 14 | | | | | | |
| 1 | 83 | 6.25 | 1.09 | -- | 33.5 | 4.03 |
| 2 | 83 | 6.32 | 1.10 | -- | 35.8 | 4.31 |
| 3 | 82 | 6.16 | 1.11 | -- | 35.8 | 4.36 |
| 4 | 84 | 6.68 | 1.12 | -- | 38.1 | 4.53 |
| 5 | 84 | 6.38 | 1.08 | -- | 38.1 | 4.53 |
| Exper. 15 | | | | | | |
| 1 | 77 | 4.90 | 1.07 | -- | 29.0 | 3.76 |
| 2 | 81 | 5.79 | 1.09 | -- | 29.0 | 3.58 |
| 3 | 83 | 6.37 | 1.11 | -- | 31.2 | 3.75 |
| 4 | 84 | 6.33 | 1.07 | -- | 33.5 | 3.98 |
| 5 | 81 | 5.61 | 1.06 | -- | 33.5 | 4.13 |
| Exper. 16 | | | | | | |
| 1 | 80 | 5.62 | 1.09 | -- | 35.8 | 4.47 |
| 2 | 83 | 6.41 | 1.12 | -- | 35.8 | 4.31 |
| 3 | 81 | 5.94 | 1.12 | -- | 38.1 | 4.70 |
| 4 | 80 | 5.78 | 1.13 | -- | 38.1 | 4.76 |
| 5 | 83 | 6.30 | 1.10 | -- | 38.1 | 4.58 |
| Exper. 17 | | | | | | |
| 1 | 81 | 5.71 | 1.07 | -- | 26.9 | 3.29 |
| 2 | 82 | 5.90 | 1.07 | -- | 26.9 | 3.25 |
| 3 | 82 | 5.89 | 1.07 | -- | 26.9 | 3.25 |
| 4 | 84 | 6.50 | 1.10 | -- | 26.9 | 3.17 |
| 5 | 82 | 6.29 | 1.14 | -- | 29.0 | 3.58 |
| Exper. 18 | | | | | | |
| 1 | 80 | 6.03 | -- | -- | 29.0 | -- |
| 2 | 83 | 6.67 | 1.17 | -- | 35.8 | 4.31 |
| 3 | 82 | 5.83 | 1.06 | -- | 38.1 | 4.64 |
| 4 | 85 | 7.18 | 1.17 | -- | 40.4 | 4.75 |
| 5 | 84 | 6.25 | 1.05 | -- | 42.7 | 5.08 |
| Exper. 19 | | | | | | |
| 1 | 80 | 5.00 | 0.98 | -- | 33.5 | 4.18 |
| 2 | 83 | 6.42 | 1.12 | -- | 35.8 | 4.31 |
| 3 | 83 | 6.00 | 1.05 | -- | 38.1 | 4.59 |
| 4 | 82 | 5.73 | 1.04 | -- | 38.1 | 4.64 |
| 5 | 81 | 5.45 | 1.02 | -- | 38.1 | 4.70 |
| Exper. 20 | | | | | | |
| 1 | 79 | 5.18 | 1.05 | 8.85 | 35.8 | 4.53 |
| 2 | 80 | 5.47 | 1.07 | 9.13 | 38.1 | 4.76 |
| 3 | 82 | 5.98 | 1.08 | 8.46 | 38.1 | 4.64 |
| 4 | 83 | 6.30 | 1.10 | 8.92 | 38.1 | 4.59 |
| 5 | 82 | 6.13 | 1.11 | 8.89 | 38.1 | 4.64 |

Table B. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 21 | | | | | | |
| 1 | 76 | 4.58 | 1.04 | 8.29 | 35.8 | 4.71 |
| 2 | 80 | 5.73 | 1.11 | -- | 38.1 | 4.76 |
| 3 | 82 | 6.19 | 1.12 | 8.01 | 40.4 | 4.92 |
| 4 | 79 | 5.80 | 1.18 | 8.25 | 42.7 | 5.40 |
| 5 | 81 | 5.62 | 1.05 | 7.54 | 42.7 | 5.27 |
| Exper. 22 | | | | | | |
| 1 | 81 | 5.70 | 1.07 | 7.58 | 35.8 | 4.41 |
| 2 | 83 | 6.18 | 1.08 | 8.04 | 35.8 | 4.31 |
| 3 | 79 | 5.61 | 1.14 | 8.50 | 35.8 | 4.53 |
| 4 | 82 | 6.32 | 1.15 | -- | 35.8 | 4.36 |
| 5 | 81 | 5.88 | 1.11 | 8.18 | 38.1 | 4.70 |
| Exper. 23 | | | | | | |
| 1 | 81 | 5.78 | 1.09 | 8.92 | 38.1 | 4.70 |
| 2 | 86 | 6.70 | 1.05 | 8.07 | 38.1 | 4.42 |
| 3 | 82 | 6.07 | 1.10 | 7.79 | 38.1 | 4.64 |
| 4 | 82 | 5.65 | 1.02 | 8.50 | 40.4 | 4.92 |
| 5 | 83 | 6.33 | 1.11 | 8.25 | 42.7 | 5.14 |
| Exper. 24 | | | | | | |
| 1 | 79 | 5.30 | 1.07 | 8.26 | 35.8 | 4.53 |
| 2 | 82 | 6.07 | 1.10 | 7.66 | 35.8 | 4.36 |
| 3 | 82 | 6.21 | 1.13 | 7.80 | 38.1 | 4.64 |
| 4 | 82 | 6.49 | 1.18 | 7.94 | 38.1 | 4.64 |
| 5 | 84 | 6.58 | 1.11 | 7.55 | 38.1 | 4.53 |
| Exper. 25 | | | | | | |
| 1 | 81 | 6.18 | 1.17 | 7.29 | 31.2 | 3.85 |
| 2 | 81 | 6.10 | 1.15 | 7.33 | 35.8 | 4.41 |
| 3 | 85 | 6.89 | 1.12 | 7.47 | 35.8 | 4.21 |
| 4 | 82 | 6.12 | 1.10 | 7.43 | 35.8 | 4.36 |
| 5 | 82 | 6.27 | 1.14 | 7.43 | 35.8 | 4.36 |
| Exper. 26 | | | | | | |
| 1 | 80 | 6.00 | 1.17 | 7.93 | 29.0 | 3.62 |
| 2 | 82 | 6.51 | 1.19 | 7.89 | 29.0 | 3.56 |
| 3 | 85 | 6.99 | 1.14 | 7.08 | 29.0 | 3.41 |
| 4 | 82 | 6.55 | 1.19 | 7.36 | 29.0 | 3.56 |
| 5 | 80 | 6.20 | 1.21 | 7.61 | 31.2 | 4.76 |
| Exper. 27 | | | | | | |
| 1 | 84 | 7.00 | 1.18 | 7.89 | 42.7 | 5.08 |
| 2 | 87 | 7.23 | 1.10 | 7.82 | 42.7 | 4.90 |
| 3 | 83 | 6.30 | 1.10 | 7.61 | 42.7 | 5.14 |
| 4 | 88 | 7.89 | 1.16 | 7.58 | 42.7 | 4.85 |
| 5 | 89 | 8.38 | 1.19 | 7.97 | 45.0 | 5.05 |

Table B. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 28 | | | | | | |
| 1 | 82 | 6.43 | 1.17 | 7.33 | 26.7 | 3.25 |
| 2 | 82 | 5.90 | 1.07 | 8.18 | 31.2 | 3.85 |
| 3 | 86 | 6.95 | 1.09 | 7.61 | 31.2 | 3.62 |
| 4 | 81 | 5.65 | 1.06 | 7.65 | 31.2 | 3.90 |
| 5 | 84 | 6.07 | 1.02 | 7.58 | 31.2 | 3.71 |
| Exper. 29 | | | | | | |
| 1 | 84 | 6.24 | 1.05 | 8.47 | 38.1 | 3.71 |
| 2 | 83 | 6.52 | 1.14 | 7.98 | 40.4 | 4.86 |
| 3 | 83 | 6.27 | 1.09 | 8.68 | 42.7 | 5.14 |
| 4 | 83 | 6.40 | 1.11 | 8.72 | 42.7 | 5.14 |
| 5 | 82 | 6.18 | 1.12 | 8.08 | 42.7 | 5.20 |
| Exper. 30 | | | | | | |
| 1 | 82 | 5.68 | 1.03 | 7.98 | 35.8 | 4.36 |
| 2 | 84 | 5.72 | 0.97 | 7.98 | 38.1 | 4.53 |
| 3 | 82 | 5.74 | 1.04 | 7.94 | 38.1 | 4.64 |
| 4 | 85 | 6.88 | 1.12 | 7.94 | 38.1 | 4.48 |
| 5 | 85 | 7.22 | 1.18 | 8.05 | 38.1 | 4.48 |
| Exper. 31 | | | | | | |
| 1 | 81 | 5.83 | 1.10 | 7.94 | 38.1 | 4.70 |
| 2 | 85 | 7.00 | 1.14 | 8.22 | 38.1 | 4.48 |
| 3 | 80 | 5.68 | 1.10 | — | 40.4 | 5.05 |
| 4 | 87 | 6.85 | 1.04 | 8.08 | 40.4 | 4.64 |
| 5 | 85 | 6.71 | 1.09 | 7.73 | 40.4 | 4.75 |
| Exper. 32 | | | | | | |
| 1 | 82 | 5.70 | 1.03 | 7.87 | 29.0 | 3.53 |
| 2 | 80 | 5.43 | 1.06 | 7.44 | 31.2 | 3.90 |
| 3 | 80 | 5.45 | 1.06 | 8.22 | 33.5 | 4.18 |
| 4 | 83 | 6.10 | 1.07 | 7.87 | 33.5 | 4.03 |
| 5 | 84 | 6.42 | 1.08 | 7.38 | 33.5 | 3.98 |
| Exper. 33 | | | | | | |
| 1 | 81 | 5.70 | 1.07 | 7.31 | 22.1 | 2.72 |
| 2 | 84 | 6.47 | 1.09 | 7.55 | 22.1 | 2.63 |
| 3 | 85 | 6.00 | 0.98 | 7.45 | 24.4 | 2.87 |
| 4 | 82 | 6.06 | 1.10 | 6.85 | 24.4 | 2.97 |
| 5 | 85 | 6.30 | 1.02 | 7.73 | 24.4 | 2.87 |

* The condition index is based on weight in grams and total length in centimeters.

Table C. Conditions of experiments with coho salmon

| Exper. Number | Date 1962 | Temperature (C°) Mean | Temperature (C°) Range | Diss. Oxygen (mg/l) | Free $CO_2$ (mg/l) | pH | Total Alkalinity (mg/l)* |
|---|---|---|---|---|---|---|---|
| 34 | 8/6 | 20.1 | 19.3-20.6 | 9.50 | 2.0 | 8.00 | 95 |
| 35 | 8/7 | 19.8 | 18.9-20.6 | 4.75 | 2.0 | 7.85 | 95 |
| 36 | 8/9 | 20.0 | 19.7-20.3 | 9.60 | 48 | 6.50 | 95 |
| 37 | 8/10 | 20.0 | 19.2-20.5 | 4.60 | 54 | 6.50 | 95 |
| 38 | 8/13 | 20.0 | 19.3-20.6 | 17.50 | 2.0 | 8.05 | |
| 39 | 8/14 | 20.1 | 19.6-20.4 | 6.10 | 1.5 | 8.15 | 103 |
| 40 | 8/15 | 19.9 | 19.2-20.3 | 11.70 | 1.6 | 8.15 | 103 |
| 41 | 8/16 | 19.7 | 19.0-20.6 | 3.40 | 1.7 | 8.15 | 103 |
| 42 | 8/17 | 20.0 | 19.8-20.4 | 25.70 | 1.7 | 8.15 | 102 |
| 43 | 8/20 | 19.9 | 19.5-20.2 | 2.20 | 1.7 | 8.15 | 104 |
| 44 | 8/21 | 20.0 | 19.7-20.6 | 2.70 | 47 | 6.65 | 100 |
| 45 | 8/22 | 19.9 | 19.3-20.4 | 24.90 | 49 | 6.60 | |
| 46 | 8/23 | 20.0 | 19.7-20.3 | 6.80 | 47 | 6.70 | 101 |
| 47 | 8/24 | 20.0 | 19.8-20.5 | 7.20 | 1.6 | 8.10 | |
| 48 | 8/27 | 20.3 | 19.4-20.4 | 2.10 | 2.0 | 8.00 | 100 |
| 49 | 9/4 | 20.3 | 19.6-20.7 | 2.10 | 48 | 6.68 | 103 |
| 50 | 9/5 | 20.0 | 19.8-20.2 | 15.30 | 50 | 6.65 | |
| 51 | 9/6 | 20.0 | 19.8-20.4 | 6.10 | 21 | 7.05 | |
| 52 | 9/7 | 20.0 | 19.7-20.2 | 9.20 | 21 | 7.05 | |
| 53 | 9/8 | 20.0 | 19.5-20.7 | 4.50 | 21 | 7.05 | |
| 54 | 9/9 | 20.0 | 20.0-20.2 | 22.80 | 20 | 7.05 | |
| 55 | 9/10 | 19.9 | 19.2-20.3 | 3.70 | 21 | 7.10 | 104 |
| 56 | 9/11 | 19.9 | 19.8-20.2 | 2.80 | 3.0 | 7.90 | |
| 57 | 9/14 | 20.1 | 19.9-20.3 | 20.15 | 3.0 | 7.95 | |
| 58 | 9/15 | 20.0 | 19.6-20.4 | 5.20 | 3.0 | 7.95 | |
| 59 | 9/16 | 20.1 | 19.9-20.4 | 2.00 | 2.0 | 8.00 | |
| 60 | 9/17 | 20.0 | 19.6-20.3 | 7.50 | 2.0 | 8.00 | |
| 61 | 9/18 | 20.1 | 19.8-20.7 | 10.35 | 2.5 | 7.92 | |
| 62 | 9/19 | 20.1 | 19.8-20.8 | 4.20 | 3.0 | 7.85 | 100 |
| 63 | 9/22 | 20.0 | 19.5-20.5 | 15.20 | 20 | 7.00 | 100 |
| 64 | 9/23 | 20.3 | 19.6-21.0 | 2.00 | 20 | 7.10 | 100 |
| 65 | 9/24 | 20.2 | 20.0-20.7 | 9.60 | 20 | 7.05 | |
| 66 | 9/25 | 19.4 | 19.0-19.7 | 4.80 | 20 | 7.78 | |
| 67 | 9/28 | 20.0 | 19.4-20.5 | 3.70 | 3.0 | 7.85 | 80 |
| 68 | 9/30 | 20.1 | 19.5-20.5 | 17.00 | 12 | 7.05 | 98 |
| 69 | 10/1 | 20.0 | 19.8-20.1 | 3.30 | 20 | 7.10 | |
| 70 | 10/2 | 20.0 | 19.7-20.3 | 6.90 | 20 | 7.10 | |

Table C. Continued

| Exper. Number | Date 1962 | Temperature (C°) Mean | Range | Diss. Oxygen (mg/l) | Free $CO_2$ (mg/l) | pH | Total Alkalinity (mg/l)* |
|---|---|---|---|---|---|---|---|
| 71 | 10/3 | 20.0 | 19.6-20.3 | 2.60 | 4.0 | 7.00 | |
| 72 | 11/2 | 20.0 | 19.8-20.5 | 3.80 | 2.0 | 8.00 | |
| 73 | 11/3 | 20.0 | 19.3-20.5 | 13.90 | 19 | 7.05 | 99 |
| 74 | 11/4 | 20.0 | 19.8-20.2 | 2.70 | 18 | 7.10 | 99 |
| 75 | 11/5 | 20.2 | 20.0-20.3 | 2.55 | 2.2 | 7.95 | |
| 76 | 11/6 | 20.2 | 20.0-20.5 | 17.60 | 50 | 6.70 | 99 |
| 77 | 11/9 | 20.1 | 19.9-20.5 | 17.80 | 3 | 7.80 | |

* Bicarbonate alkalinity expressed as the calcium carbonate ($CaCO_3$) equivalent. Total dissolved solids ranged between 130 and 167 mg/l.

Table D. Descriptive data on individual coho salmon and their maximum swimming speeds at which failure occurred (in centimeters per second and lengths per second). Fish are numbered in the order of their failure in each experiment.

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 34 | | | | | | |
| 1 | 83 | 4.62 | 1.01 | 7.87 | 41.1 | 4.93 |
| 2 | 81 | 3.70 | 0.88 | 7.23 | 52.6 | 6.48 |
| 3 | 81 | 4.15 | 0.98 | 7.48 | 57.2 | 7.05 |
| 4 | 85 | 5.71 | 1.16 | 7.69 | 59.4 | 6.95 |
| 5 | 92 | 6.78 | 1.10 | 8.08 | 61.7 | 6.71 |
| Exper. 35 | | | | | | |
| 1 | 81 | 4.37 | 1.04 | 7.16 | 45.7 | 5.63 |
| 2 | 82 | 4.34 | 0.98 | 7.37 | 50.3 | 6.11 |
| 3 | 79 | 4.33 | 1.11 | 6.00 | 50.3 | 6.37 |
| 4 | 89 | 4.85 | 0.88 | 8.96 | 54.9 | 6.19 |
| 5 | 85 | 5.34 | 1.08 | 6.03 | 54.9 | 6.42 |
| Exper. 36 | | | | | | |
| 1 | 86 | 5.47 | 1.07 | 6.81 | 41.1 | 4.74 |
| 2 | 81 | 3.98 | 0.94 | 5.85 | 41.1 | 5.06 |
| 3 | 91 | 5.48 | 0.92 | 7.76 | 41.1 | 4.52 |
| 4 | 89 | 5.31 | 0.96 | 6.84 | 48.0 | 5.41 |
| 5 | 81 | 4.71 | 1.11 | 6.24 | 50.3 | 6.19 |
| Exper. 37 | | | | | | |
| 1 | 81 | 4.19 | 0.99 | 6.21 | 36.6 | 4.51 |
| 2 | 83 | 5.05 | 1.11 | 6.81 | 41.1 | 4.93 |
| 3 | 79 | 4.35 | 1.11 | 6.00 | 41.1 | 5.20 |
| 4 | 79 | 4.58 | 1.18 | 6.74 | 41.1 | 5.20 |
| 5 | 81 | 4.40 | 1.04 | 5.04 | 45.7 | 5.63 |
| Exper. 38 | | | | | | |
| 1 | 79 | 4.59 | 1.18 | 7.06 | 50.3 | 6.36 |
| 2 | 81 | 4.18 | 0.99 | 6.17 | 54.9 | 6.76 |
| 3 | 79 | 4.65 | 1.20 | 6.98 | 57.2 | 7.24 |
| 4 | 81 | 5.05 | 1.20 | 6.98 | 61.7 | 7.60 |
| 5 | 80 | 4.70 | 1.16 | 6.45 | 64.0 | 7.99 |
| Exper. 39 | | | | | | |
| 1 | 81 | 4.32 | 1.02 | 5.22 | 48.0 | 5.91 |
| 2 | 81 | 4.75 | 1.13 | 5.64 | 52.6 | 6.48 |
| 3 | 81 | 4.87 | 1.15 | 6.88 | 52.6 | 6.48 |
| 4 | 81 | 4.80 | 1.14 | 6.38 | 57.2 | 7.05 |
| 5 | 84 | 4.80 | 1.01 | 6.07 | 59.4 | 7.04 |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 40 | | | | | | |
| 1 | 86 | 5.66 | 1.10 | 8.47 | 54.9 | 6.34 |
| 2 | 100 | 7.92 | 0.98 | 8.61 | 61.7 | 6.13 |
| 3 | 90 | 6.30 | 1.10 | 8.15 | 64.0 | 7.13 |
| 4 | 93 | 6.55 | 1.03 | 8.82 | | |
| 5 | 90 | 5.80 | 1.01 | 8.04 | | |
| Exper. 41 | | | | | | |
| 1 | 85 | 5.40 | 1.09 | 6.70 | 34.3 | 4.01 |
| 2 | 86 | 4.95 | 0.96 | 8.26 | 38.9 | 4.49 |
| 3 | 88 | 6.12 | 1.15 | 5.75 | 41.1 | 4.69 |
| 4 | 87 | 6.10 | 1.19 | 7.48 | 41.1 | 4.74 |
| 5 | 87 | 5.38 | 1.05 | 7.02 | 41.1 | 4.74 |
| Exper. 42 | | | | | | |
| 1 | 80 | 4.50 | 1.11 | 7.94 | 54.9 | 6.85 |
| 2 | 86 | 5.31 | 1.04 | 7.76 | 57.2 | 6.61 |
| 3 | 83 | 5.08 | 1.11 | 8.11 | 57.2 | 6.86 |
| 4 | 85 | 5.00 | 1.01 | 8.22 | 59.4 | 6.95 |
| 5 | 85 | 5.08 | 1.03 | 6.98 | 59.4 | 6.95 |
| Exper. 43 | | | | | | |
| 1 | 83 | 4.81 | 1.05 | 6.67 | 29.7 | 3.56 |
| 2 | 86 | 4.80 | 0.94 | 6.67 | 29.7 | 3.43 |
| 3 | 80 | 4.63 | 1.14 | 6.63 | 29.7 | 3.71 |
| 4 | 82 | 4.25 | 0.97 | 6.53 | 34.3 | 4.17 |
| 5 | 89 | 5.97 | 1.08 | 6.74 | 36.6 | 4.12 |
| Exper. 44 | | | | | | |
| 1 | 81 | 4.80 | 1.14 | 5.73 | 32.0 | 3.94 |
| 2 | 78 | 4.37 | 1.17 | 6.83 | 34.3 | 4.40 |
| 3 | 84 | 5.20 | 1.10 | 6.63 | 36.6 | 4.33 |
| 4 | 80 | 4.40 | 1.09 | 6.23 | 36.6 | 4.57 |
| 5 | 85 | 4.71 | 0.95 | 6.72 | 38.9 | 4.55 |
| Exper. 45 | | | | | | |
| 1 | 82 | 4.23 | 0.96 | 8.01 | 43.4 | 5.27 |
| 2 | 79 | 3.95 | 1.06 | 6.74 | 45.7 | 5.86 |
| 3 | 81 | 4.77 | 1.13 | 5.87 | 48.0 | 5.91 |
| 4 | 81 | 4.51 | 1.07 | 6.72 | 52.6 | 6.48 |
| 5 | 81 | 4.68 | 1.11 | 6.72 | 54.9 | 6.76 |
| Exper. 46 | | | | | | |
| 1 | 79 | 4.13 | 1.06 | 7.19 | 41.1 | 5.20 |
| 2 | 79 | 3.85 | 0.99 | 7.22 | 48.0 | 6.07 |
| 3 | 77 | 4.12 | 1.15 | 6.62 | 50.3 | 6.54 |
| 4 | 78 | 4.42 | 1.18 | 6.72 | 50.3 | 6.45 |
| 5 | 76 | 3.28 | 0.96 | 6.37 | 57.2 | 7.55 |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 47 | | | | | | |
| 1 | 84 | 4.86 | 1.02 | 7.76 | 59.4 | 7.04 |
| 2 | 83 | 4.90 | 1.07 | 7.26 | 59.4 | 7.13 |
| 3 | 86 | 5.13 | 1.01 | 7.51 | 61.7 | 7.13 |
| 4 | 88 | 5.70 | 1.07 | 7.68 | 61.7 | 7.04 |
| 5 | 84 | 5.09 | 1.07 | 6.08 | 61.7 | 7.31 |
| Exper. 48 | | | | | | |
| 1 | 84 | 5.03 | 1.06 | 7.22 | 25.1 | 2.97 |
| 2 | 83 | 4.92 | 1.08 | 6.87 | 27.4 | 3.28 |
| 3 | 84 | 4.70 | 0.99 | 7.47 | 27.4 | 3.24 |
| 4 | 90 | 6.00 | 1.05 | 7.12 | 27.4 | 3.05 |
| 5 | 83 | 4.81 | 1.05 | 7.08 | 32.0 | 3.84 |
| Exper. 49 | | | | | | |
| 1 | 89 | 6.38 | 1.16 | 7.01 | 27.4 | 3.08 |
| 2 | 86 | 5.40 | 1.05 | 7.58 | 29.7 | 3.43 |
| 3 | 85 | 5.42 | 1.10 | 6.79 | 32.0 | 3.74 |
| 4 | 81 | 5.08 | 1.20 | 6.33 | 32.0 | 3.94 |
| 5 | 85 | 5.25 | 1.06 | 6.90 | 32.0 | 3.74 |
| Exper. 50 | | | | | | |
| 1 | 92 | 6.87 | 1.12 | 7.61 | 41.1 | 4.47 |
| 2 | 85 | 5.48 | 1.11 | 7.68 | 52.6 | 6.15 |
| 3 | 96 | 7.95 | 1.13 | 7.08 | 59.4 | 6.17 |
| 4 | 94 | 7.23 | 1.10 | 7.90 | 61.7 | 6.55 |
| 5 | 96 | 7.10 | 1.01 | 7.19 | 66.3 | 6.88 |
| Exper. 51 | | | | | | |
| 1 | 91 | 6.20 | 1.05 | 8.40 | 45.7 | 5.03 |
| 2 | 83 | 4.93 | 1.08 | 7.54 | 54.9 | 6.59 |
| 3 | 93 | 6.85 | 1.08 | 7.44 | 54.9 | 5.90 |
| 4 | 85 | 5.10 | 1.04 | 6.37 | 59.4 | 6.95 |
| 5 | 91 | 6.20 | 1.05 | 7.90 | 64.0 | 7.04 |
| Exper. 52 | | | | | | |
| 1 | 79 | 4.39 | 1.13 | 7.12 | 52.6 | 6.66 |
| 2 | 82 | 4.41 | 1.00 | 7.51 | 54.9 | 6.67 |
| 3 | 82 | 5.02 | 1.14 | 7.29 | 59.4 | 7.22 |
| 4 | 83 | 4.70 | 1.03 | 7.86 | 61.7 | 7.40 |
| 5 | 84 | 5.31 | 1.12 | 7.19 | 64.0 | 7.58 |
| Exper. 53 | | | | | | |
| 1 | 83 | 4.49 | 0.98 | 6.62 | 43.4 | 5.21 |
| 2 | 77 | 4.21 | 1.18 | 5.73 | 48.0 | 6.24 |
| 3 | 80 | 4.39 | 1.08 | 5.94 | 48.0 | 5.99 |
| 4 | 83 | 4.68 | 1.02 | 7.01 | 54.9 | 6.59 |
| 5 | 80 | 4.25 | 1.05 | 6.26 | 54.9 | 6.85 |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 54 | | | | | | |
| 1 | 81 | 4.81 | 1.14 | 8.18 | 52.6 | 6.48 |
| 2 | 79 | 4.41 | 1.13 | 5.73 | 57.2 | 7.24 |
| 3 | 84 | 4.87 | 1.03 | 7.83 | 57.2 | 6.77 |
| 4 | 80 | 4.26 | 1.05 | 6.26 | 57.2 | 7.14 |
| 5 | 84 | 5.28 | 1.11 | 7.22 | 64.0 | 7.58 |
| Exper. 55 | | | | | | |
| 1 | 81 | 4.40 | 1.04 | 7.04 | 41.1 | 5.06 |
| 2 | 79 | 4.00 | 1.03 | 6.33 | 43.4 | 5.49 |
| 3 | 80 | 4.33 | 1.07 | 6.90 | 45.7 | 5.70 |
| 4 | 82 | 4.68 | 1.06 | 8.29 | 48.0 | 5.83 |
| 5 | 81 | 4.40 | 1.04 | 5.83 | 48.0 | 5.91 |
| Exper. 56 | | | | | | |
| 1 | 80 | 4.27 | 1.05 | 7.90 | 36.6 | 4.57 |
| 2 | 79 | 4.46 | 1.15 | 5.90 | 36.6 | 4.63 |
| 3 | 79 | 4.32 | 1.11 | 8.11 | 38.9 | 4.92 |
| 4 | 80 | 4.47 | 1.10 | 6.44 | 41.1 | 5.13 |
| 5 | 80 | 3.95 | 0.97 | 7.93 | 43.4 | 5.42 |
| Exper. 57 | | | | | | |
| 1 | 78 | 4.10 | 1.10 | 7.90 | 52.6 | 6.75 |
| 2 | 76 | 3.55 | 1.03 | 7.01 | 57.2 | 7.55 |
| 3 | 78 | 4.08 | 1.09 | 7.01 | 61.7 | 7.92 |
| 4 | 74 | 3.51 | 1.12 | 6.87 | 61.7 | 8.38 |
| 5 | 82 | 4.63 | 1.05 | 6.47 | 66.3 | 8.06 |
| Exper. 58 | | | | | | |
| 1 | 78 | 4.40 | 1.18 | 6.79 | 41.1 | 5.27 |
| 2 | 80 | 4.18 | 1.03 | 6.90 | 54.9 | 6.85 |
| 3 | 81 | 4.41 | 1.04 | 5.98 | 57.2 | 7.05 |
| 4 | 81 | 4.50 | 1.07 | 6.19 | 57.2 | 7.05 |
| 5 | 82 | 4.67 | 1.06 | 7.26 | 57.2 | 6.95 |
| Exper. 59 | | | | | | |
| 1 | 89 | 5.70 | 1.03 | 6.55 | 27.4 | 3.08 |
| 2 | 84 | 4.65 | 0.98 | 8.22 | 32.0 | 3.79 |
| 3 | 89 | 5.70 | 1.03 | 7.01 | 32.0 | 3.60 |
| 4 | 86 | 5.02 | 0.98 | 7.08 | 36.6 | 4.22 |
| 5 | 84 | 5.08 | 1.07 | 7.26 | 36.6 | 4.33 |
| Exper. 60 | | | | | | |
| 1 | 85 | 4.96 | 1.01 | 5.87 | 57.2 | 6.69 |
| 2 | 86 | 5.37 | 1.05 | 7.11 | 61.7 | 7.13 |
| 3 | 84 | 4.68 | 0.99 | 7.07 | 64.0 | 7.58 |
| 4 | 86 | 5.51 | 1.08 | 6.26 | 70.9 | 8.19 |
| 5 | 81 | 4.51 | 1.07 | 6.96 | | |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 61 | | | | | | |
| 1 | 82 | 5.62 | 1.02 | 7.95 | 52.6 | 5.93 |
| 2 | 80 | 5.50 | 1.07 | 6.33 | 64.0 | 7.39 |
| 3 | 85 | 6.40 | 1.04 | 7.35 | 70.9 | 7.71 |
| 4 | 83 | 6.10 | 1.07 | 8.30 | 70.9 | 7.90 |
| 5 | 81 | 5.67 | 1.07 | 7.14 | 70.9 | 8.09 |
| Exper. 62 | | | | | | |
| 1 | 80 | 4.70 | 0.92 | 6.40 | 50.3 | 5.81 |
| 2 | 79 | 4.45 | 0.90 | 7.25 | 52.6 | 6.15 |
| 3 | 80 | 5.75 | 1.12 | 6.05 | 54.9 | 6.34 |
| 4 | 83 | 5.55 | 0.97 | 7.25 | 54.9 | 6.12 |
| 5 | 78 | 5.00 | 1.05 | 7.77 | 59.4 | 7.04 |
| Exper. 63 | | | | | | |
| 1 | 74 | 4.10 | 1.01 | 6.61 | 43.4 | 5.42 |
| 2 | 78 | 5.17 | 1.09 | 6.01 | 57.2 | 6.77 |
| 3 | 73 | 4.18 | 1.07 | 6.79 | 59.4 | 7.52 |
| 4 | 81 | 5.62 | 1.06 | 8.13 | 61.7 | 7.04 |
| 5 | 82 | 5.79 | 1.05 | 6.19 | 64.0 | 7.21 |
| Exper. 64 | | | | | | |
| 1 | 73 | 4.53 | 1.16 | | 22.8 | |
| 2 | 73 | 4.51 | 1.16 | 6.65 | 27.4 | 3.46 |
| 3 | 78 | 4.88 | 1.03 | 7.07 | 32.0 | 3.79 |
| 4 | 77 | 4.82 | 1.06 | 7.14 | 34.3 | 4.11 |
| 5 | 74 | 4.30 | 1.06 | 6.54 | 34.3 | 4.28 |
| Exper. 65 | | | | | | |
| 1 | 70 | 3.70 | 1.08 | 6.96 | 41.1 | 5.42 |
| 2 | 75 | 4.41 | 1.04 | 5.94 | 52.6 | 6.48 |
| 3 | 72 | 3.82 | 1.02 | 6.86 | 54.9 | 7.04 |
| 4 | 72 | 3.72 | 1.00 | 5.94 | 57.2 | 7.34 |
| 5 | 72 | 4.28 | 1.15 | 5.94 | | |
| Exper. 66 | | | | | | |
| 1 | 74 | 3.80 | 0.94 | | 41.1 | 5.13 |
| 2 | 75 | 3.41 | 0.80 | | 43.4 | 5.34 |
| 3 | 77 | 3.88 | 0.85 | | 45.7 | 5.48 |
| 4 | 73 | 3.82 | 0.98 | | 48.0 | 6.07 |
| 5 | 79 | 5.10 | 1.03 | | 54.9 | 6.42 |
| Exper. 67 | | | | | | |
| 1 | 73 | 3.57 | 0.92 | 6.96 | 38.9 | 4.92 |
| 2 | 73 | 4.05 | 1.04 | 7.95 | 41.1 | 5.20 |
| 3 | 81 | 5.60 | 1.05 | 6.86 | 43.4 | 4.95 |
| 4 | 75 | 4.46 | 1.06 | 7.04 | 45.7 | 5.63 |
| 5 | 72 | 3.99 | 1.07 | 6.23 | 45.7 | 5.86 |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 68 | | | | | | |
| 1 | 68 | 3.21 | 1.02 | | 36.6 | 4.97 |
| 2 | 69 | 3.58 | 1.09 | | 38.9 | 5.21 |
| 3 | 70 | 3.33 | 0.97 | | 41.1 | 5.42 |
| 4 | 71 | 3.87 | 1.08 | 6.72 | 48.0 | 6.24 |
| 5 | 70 | 3.57 | 1.04 | 7.11 | 57.2 | 7.55 |
| Exper. 69 | | | | | | |
| 1 | 67 | 3.23 | 1.07 | 6.44 | 32.0 | 4.41 |
| 2 | 73 | 4.22 | 1.08 | 7.88 | 38.9 | 4.92 |
| 3 | 72 | 4.09 | 1.10 | 6.79 | 43.4 | 5.57 |
| 4 | 72 | 3.82 | 1.02 | | 43.4 | 5.57 |
| 5 | 74 | 4.23 | 1.04 | 6.58 | 45.7 | 5.70 |
| Exper. 70 | | | | | | |
| 1 | 75 | 3.91 | 0.93 | | 43.4 | 5.34 |
| 2 | 74 | 3.88 | 0.96 | | 50.3 | 6.28 |
| 3 | 73 | 3.78 | 0.97 | | 54.9 | 6.95 |
| 4 | 72 | 3.81 | 1.02 | | 54.9 | 7.04 |
| 5 | 76 | 4.63 | 1.05 | | 59.4 | 7.22 |
| Exper. 71 | | | | | | |
| 1 | 71 | 3.70 | 1.03 | 6.89 | 32.0 | 4.16 |
| 2 | 72 | 3.67 | 0.98 | | 34.3 | 4.40 |
| 3 | 70 | 3.60 | 1.05 | | 36.6 | 4.83 |
| 4 | 71 | 3.70 | 1.03 | 6.37 | 36.6 | 4.76 |
| 5 | 70 | 3.58 | 1.04 | 6.33 | 38.9 | 5.13 |
| Exper. 72 | | | | | | |
| 1 | 75 | 4.22 | 1.00 | | 43.4 | 5.34 |
| 2 | 75 | 3.83 | 0.91 | | 43.4 | 5.34 |
| 3 | 70 | 3.60 | 1.05 | | 48.0 | 6.33 |
| 4 | 72 | 3.67 | 0.98 | | 48.0 | 6.16 |
| 5 | 77 | 4.65 | 1.02 | | 50.3 | 6.03 |
| Exper. 73 | | | | | | |
| 1 | 79 | 4.81 | 0.98 | 6.01 | 52.6 | 6.15 |
| 2 | 78 | 4.30 | 0.91 | 6.12 | 57.2 | 6.77 |
| 3 | 72 | 3.95 | 1.06 | 6.15 | 57.2 | 7.34 |
| 4 | 77 | 3.98 | 0.87 | 6.62 | 57.2 | 6.86 |
| 5 | 73 | 3.67 | 0.94 | 6.33 | 59.4 | 7.52 |
| Exper. 74 | | | | | | |
| 1 | 70 | 3.44 | 1.00 | 4.79 | 32.0 | 4.22 |
| 2 | 73 | 3.82 | 0.98 | 5.22 | 32.0 | 4.05 |
| 3 | 72 | 3.65 | 0.98 | 5.29 | 36.6 | 4.69 |
| 4 | 81 | 5.00 | 0.95 | 5.65 | 41.1 | 4.69 |
| 5 | 78 | 4.39 | 0.92 | 5.51 | 41.1 | 4.87 |

Table D. Continued

| Exper. No. and Fish No. | Total Length (mm.) | Weight (grams) | Condition Index* | Hemoglobin (g/100 ml) | Swimming Speed cm/sec | Swimming Speed L/sec |
|---|---|---|---|---|---|---|
| Exper. 75 | | | | | | |
| 1 | 77 | 4.73 | 1.04 | 5.76 | 34.3 | 4.11 |
| 2 | 76 | 4.68 | 1.07 | 4.33 | 36.6 | 4.45 |
| 3 | 81 | 5.38 | 1.01 | 5.26 | 38.9 | 4.44 |
| 4 | 78 | 4.62 | 0.97 | 5.37 | 38.9 | 4.61 |
| 5 | 72 | 3.88 | 1.04 | 5.11 | 38.9 | 4.99 |
| Exper. 76 | | | | | | |
| 1 | 80 | 5.30 | 1.04 | | 57.2 | 6.60 |
| 2 | 79 | 4.90 | 0.99 | | 59.4 | 6.94 |
| 3 | 80 | 5.20 | 1.02 | | 59.4 | 6.86 |
| 4 | 79 | 5.13 | 1.04 | | 61.7 | 7.21 |
| 5 | 82 | 5.00 | 0.91 | | 64.0 | 7.21 |
| Exper. 77 | | | | | | |
| 1 | 75 | 4.40 | 1.04 | | 59.4 | 7.32 |
| 2 | 77 | 4.67 | 1.02 | | 64.0 | 7.70 |
| 3 | 74 | 4.29 | 1.06 | | 66.3 | 8.28 |
| 4 | 78 | 5.30 | 1.12 | | 66.3 | 7.85 |
| 5 | 76 | 4.65 | 1.06 | | 66.3 | 7.85 |

* The condition index is based on weight in grams and fork length in centimeters.