

# The Influence of Oxygen Concentration on the Swimming Performance of Juvenile Pacific Salmon at Various Temperatures<sup>1 2</sup>

GERALD E. DAVIS,<sup>3</sup> JACK FOSTER,<sup>3</sup> CHARLES E. WARREN,<sup>3</sup> AND PETER DOUDOROFF<sup>4</sup>  
*Pacific Cooperative Water Pollution and Fisheries Research Laboratories (Oregon State University and U. S. Public Health Service), Oregon State University, Corvallis, Oregon*

## ABSTRACT

The sustained swimming speeds of juvenile coho and chinook salmon tested in a tubular chamber at temperatures ranging from 10 to 20° C. usually were dependent on the dissolved oxygen concentration at any tried concentration below the air-saturation level. Some underyearling chinook salmon tested at 19.5° C. were notably exceptional; their performance at high oxygen concentrations was not markedly better than that observed at lower concentrations between 5 and 7 mg/l. These fish may have been anemic. Reduction of oxygen concentration from air-saturation levels to 7, 6, 5, 4, and 3 mg/l usually resulted in reduction of the maximum sustained swimming speed of coho salmon by about 5, 8, 13, 20, and 30 percent, respectively. These percentages are based on the observed performance of the first-failing and second-failing individuals of a group of five fish used in a performance test. The corresponding estimated percent reductions of the swimming speed of first-failing fish in most of the early exploratory experiments with chinook salmon were somewhat greater, averaging approximately 10, 14, 20, 27, and 38 percent, respectively. Within the ranges of tested concentrations above the saturation levels, variations of oxygen concentration had little or no effect on the performance of wild underyearling and hatchery-reared yearling coho salmon. The performance of the wild underyearlings at tested oxygen concentrations improved progressively with increase of temperature from 10 to 15 and to 20° C.

## INTRODUCTION

Many experiments at various temperatures have been reported in which mortalities of resting fish and oxygen consumption rates of both resting and active fish have been related to oxygen concentration. Few experiments have been reported, however, on the influence of reduced levels of dissolved oxygen on growth and on swimming performance. The need for such information in determining the water quality requirements of fish and controlling water pollution has been emphasized by Doudoroff (1957, 1960) and others.

Katz, Pritchard, and Warren (1959) have demonstrated the ability of juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), and chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), to swim for 24 or 48 hours at the moderate speed of 0.8 foot per second in water at 20° C. with oxygen concentrations near 3 mg/l, not much above the concentrations which would be lethal to these fish under

conditions necessitating no sustained activity. Graham (1949) has reported one experiment with three fish on the influence of oxygen concentration on the maximum steady swimming or "cruising" speed of the brook trout, *Salvelinus fontinalis* (Mitchill), at 8° C. Fry (1957) has reported some previously unpublished results of similar experiments at several temperatures with the yellow perch, *Perca flavescens* (Mitchill), performed by R. G. Ferguson. Marked reduction of the cruising speeds of both trout and perch at low oxygen concentrations was demonstrated, but in the case of the brook trout, only concentrations below 6 mg/l were found to have any effect.

The influence of temperature on the cruising speed of goldfish, *Carassius auratus* (Linnaeus), has been studied by Fry and Hart (1948). Similar experiments with coho salmon and sockeye salmon, *Oncorhynchus nerka* (Walbaum), have been reported by Brett, Hollands, and Alderdice (1958). The optimal temperature for the performance of the coho salmon was found to be near 20° C.

The influence of reduced oxygen concentration on the survival of juvenile coho salmon at different temperatures and on their food consumption and growth at temperatures near 20° C. has been investigated (Davison *et al.*, 1959; Herrmann, Warren, and Doudoroff,

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<sup>3</sup>Department of Fish and Game Management, Oregon State University.

<sup>4</sup>Robert A. Taft Sanitary Engineering Center, U. S. Public Health Service.

1962). The growth and food consumption rates of abundantly fed underyearlings declined slightly with reduction of oxygen concentration to 6 and 5 mg/l, and declined more sharply with further reduction of oxygen concentration.

The purpose of the present investigation was to determine the extent to which the maximum sustained swimming speeds of juvenile coho and chinook salmon at selected temperatures ranging from 10 to 20° C. are reduced by reduction of oxygen concentration to various levels below the air-saturation levels. Tests at oxygen concentrations above the air-saturation level sometimes were performed in order to determine whether the best swimming performance of which the fish were capable at a given test temperature had or had not been attained at the saturation level. The data from the experiments with coho salmon reported herein have been presented more fully in tabular form by Davis.<sup>5</sup>

#### MATERIALS AND METHODS

##### *Experimental fish*

Underyearling coho salmon were seined from tributaries of the Alsea and Yaquina Rivers in Lincoln County, Oregon. One group of yearling coho salmon was obtained from the Oregon Fish Commission's Fall Creek Salmon Hatchery in the Alsea River basin, and another was taken from an experimental rearing pond on Mill Creek, a tributary of the Alsea River. The latter fish had been obtained as fry from the Fall Creek Hatchery, but had not been fed before planting in the rearing pond, where they subsisted entirely on natural food. Underyearling and yearling chinook salmon were obtained from the Oregon Fish Commission's McKenzie River Salmon Hatchery in Lane County. Underyearlings tested at 15° C. in May and June of 1958 had been obtained from the hatchery in March when they were very small. They were held at the laboratory for more than 6 weeks before the tests were begun, and during this period they grew large enough to use in the experimental apparatus. All the fish were graded according

to size, the largest and smallest individuals being discarded.

The coho salmon were held in round, wooden, outdoor stock tanks, 60 inches in diameter and 24 inches deep, at the Oak Creek Laboratory near Corvallis. The tanks were supplied with water from a small spring-fed stream. Water from the same source was filtered and used in the experimental apparatus in all tests with coho salmon. Chinook salmon used in experiments at 19.5° C. also were held in a stock tank at the Oak Creek Laboratory. Those used in other experiments were held in similar tanks at the Squaw Creek Laboratory, Corvallis, which were supplied with water from Marys River. Water from the latter source was used (after filtration when turbid) in all the tests with chinook salmon.

All chinook salmon that were tested at 19.5° C. were held for 3 to 5 days in standing aerated water in a 20° C. constant-temperature room at the Squaw Creek Laboratory before their use in each test. With this exception, the experimental animals were not specially acclimatized to the test temperatures before their introduction into the experimental apparatus. However, experiments at each test temperature except temperatures near 20° C. were performed during a period or season in which the mean recorded temperature of the water in the stock tanks did not differ by much more than 3° C. from the test temperature. Thus, stock tank temperatures recorded when wild underyearling coho salmon were removed for testing at 10° and 15° C. averaged 7.5° (range 5.3–11.1°) and 15.0° (range 12.6–18.6°), respectively; and those recorded when yearling cohos were removed for testing at 12° and 15° C. averaged 8.7° (range 6.4–11.9°) and 13.0° (range 11.1–15.6°), respectively. Stock tank temperatures recorded when the underyearling cohos were removed for testing at 20° C. were all well below the test temperature (range 8.2–15.0°) and averaged 12.3° C.

The underyearling coho salmon were fed a ground diet composed of 70 percent marine fish of several species, 8 percent horse meat, 10 percent beef tripe, 3 percent beef liver, and 9 percent cereals. The yearling coho salmon and the chinook salmon were fed beef liver with a dried meal supplement and salt.

<sup>5</sup> Davis, G. E. (1960) The influence of dissolved oxygen concentration on the swimming performance of juvenile coho salmon at different temperatures. M.S. thesis, Oregon State University, 58 pp.

confined in a horizontal glass tube ("Pyrex" glass pipe) 60 inches long and 4 inches in diameter. Water could be continually circulated through this tubular chamber by means of a centrifugal pump capable of producing currents with velocities up to 2.5 feet per second (f.p.s.). The velocities were adjustable by means of a calibrated gate valve located at the pump's outlet. Three circular wire-mesh screens of varying diameter attached inside the tube near the upstream end served as baffles for distributing the flow of water from the pump and dissipating gross turbulence or reducing it to finer patterns. The observed motion of particles suspended in the water and the behavior of test animals indicated that a fairly well distributed and rectilinear flow thus was produced in the tube, except in the immediate vicinity of the baffles. A movable screen (perforated aluminum plate) served as a closure near the downstream end of the tube. This screen was mounted on a retractile rod and could be positioned so as to permit introduction of fish into the tube through a funnel-like receptacle, or removal of water and fish through a stoppered outlet.

The water in the system was replaced continually, at a rate of about 1 liter per minute, with fresh water of adjusted temperature and oxygen content. The incoming water was heated to the desired temperature by means of a thermostatically controlled heater immersed in a glass jar. The dissolved oxygen content was regulated by bubbling nitrogen, air, or oxygen at an appropriate rate through the water as it flowed downward in an overflowing glass column filled with Raschig rings. The flow of nitrogen or oxygen through the column was adjusted by means of a two-stage pressure-reducing valve. The flow of water through the column and into the tubular chamber was regulated by adjusting the level at which water left the system, *i.e.*, by raising or lowering the distal end of a rubber tube serving as an outlet. The water entering and leaving the tubular chamber passed through sample bottles which could be withdrawn for determination of the oxygen content of the water.

The temperature of the water circulating in the system increased in the pump because of fluid friction. Compensatory cooling of the

water was achieved by passing it through an aluminum heat exchanger. The heat exchanger was immersed in one of two adjacent compartments of a partitioned tank filled with a cooled, circulated, aqueous solution of ethylene glycol. From this compartment of the tank, the solution was transferred by means of two small pumps to the other compartment containing the cooling coils of a refrigeration unit; the colder solution so displaced overflowed into the former compartment (*i.e.*, returned) through a notch in the tank's partition. Valves at the pump outlets regulated the transfer rates. One pump operated continuously, whereas the other was activated by a thermoregulator immersed in the water flowing out of the tubular chamber. The water flowing through the chamber thus was kept automatically at a fairly uniform temperature. The range of temperature fluctuation usually was less than  $1.5^{\circ}$  C., but brief failures of the thermoregulatory system resulted in larger fluctuations up to about  $2.5^{\circ}$  C. on rare occasions.

An indicator on the handwheel of the gate valve used for regulating water velocities and a graduated dial (not shown in Figure 1 of the cited drawing) facilitated accurate velocity adjustment. The valve was calibrated with a Stevens Midget Current Meter, manufactured by Leupold and Stevens Instruments, Inc. Portland, Oregon. Calibration was repeated during the course of the experiments, and the curve relating valve settings to current velocities was found to be unchanged.

### *Experimental procedure*

The procedures followed were essentially uniform throughout the study. Test fish were not fed on the day of their removal from a stock tank for transfer to the experimental apparatus. The transfer took place in the afternoon or early evening of the day preceding the day of the test. The temperature of the water in the apparatus then was about the same as that of the water from which the fish had been taken. A group of five fish of uniform size was used in each test.

As soon as the introduced fish were calm the water velocity in the tubular chamber was slowly increased to 0.25 f.p.s., and the aut-

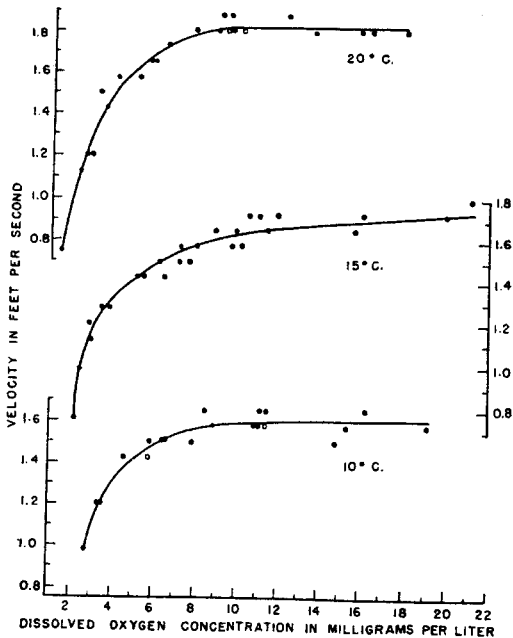


FIGURE 2.—Water velocities at which swimming failures of first-failing wild underyearling coho salmon occurred at 10, 15, and 20° C., in relation to dissolved oxygen concentration.

ent, for this would have made it possible for all or most of the fish frequently to occupy unduly favorable situations, avoiding the full, rated, current velocities.

Coho salmon seldom remained in the supposedly favorable positions at the upstream end of the test chamber. Therefore, when small underyearling cohos were used as test animals, the water velocity resulting in failure of the third fish of five probably could have been profitably determined; however, this was not done, so that data pertaining to first and second failures only are available. The presence on the downstream closure of even a single fish perhaps had some slight effect on conditions in the test chamber (current velocity, etc.); thus the first-failure data are deemed somewhat more reliable than the second-failure data.

Some comparative measurements were made of the hemoglobin content of the blood of the yearling and underyearling coho salmon from different sources by the colorimetric acid hematin method. For such a determination, a 0.025-milliliter sample of blood taken from the caudal artery of a fish whose tail had been severed was drawn into a blood-diluting pipette and hemolized in 5 milliliters of 0.1 normal hydrochloric acid. The light-transmittancy of the diluted blood sample was determined electrophotometrically, employing a filter with a wavelength rating of 525 millimicrons. The Fisher Electrophotometer employed was calibrated using a Bausch and Lomb "Spectronic 20" Colorimeter and an available table (in Bausch and Lomb's *Methods and Calibrations* manual) relating transmittancy readings made with the latter instrument to hemoglobin levels in grams per 100 milliliters of blood.

The acid hematin method employed is not entirely satisfactory for determination of hemoglobin in fish blood because nuclei of erythrocytes remain in suspension. The uncorrected hemoglobin values reported herein may all be too high (Larsen and Snieszko, 1961).<sup>6</sup> These values are deemed sufficiently instructive, however, and usable without correction for present comparative purposes.

<sup>6</sup> Larsen and Snieszko (1961) have suggested the following "factor" or formula for correcting the standard acid hematin hemoglobin (A-H Hb) values obtained with trout blood:

$$0.534 \times \text{A-H Hb} + 2.44.$$

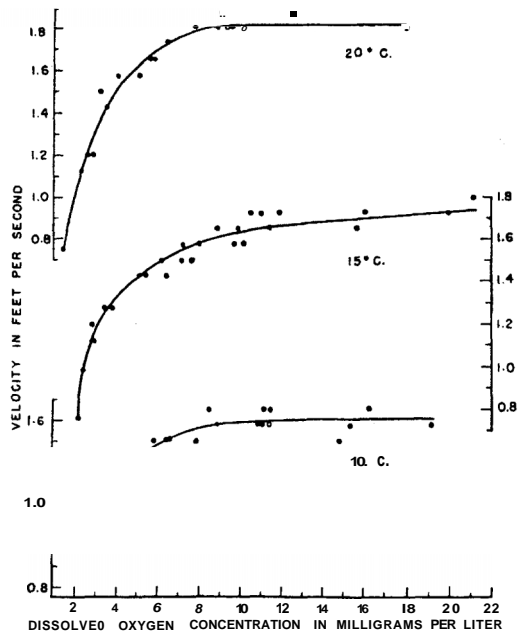


FIGURE 2.--Water velocities at which swimming failures of first-failing wild underyearling coho salmon occurred at 10, 15, and 20°C., in relation to dissolved oxygen concentration.

## RESULTS

### *Underyearling coho salmon*

The results of experiments with wild underyearling coho salmon (for dates, see Table 1) at temperatures near 10, 15, and 20° C. (Figures 2 and 3) are the ones deemed most consistent and satisfactory, and will be considered first. The experiments showed that at each test temperature the swimming performance of the coho salmon was dependent upon the dissolved oxygen concentration throughout or nearly throughout the range of tested concentrations below the air-saturation level. Within the range of tested concentrations above the saturation value, variations of oxygen concentration had only little or no effect on the performance. At any oxygen concentration within the experimental range, the performance capability of the fish proved greater at the highest test temperature (20° C.) than at the lower temperatures.

In Figure 2, which shows the relation between oxygen concentration and water velocities resulting in first failures at each test temperature, all points obtained in the usual man-

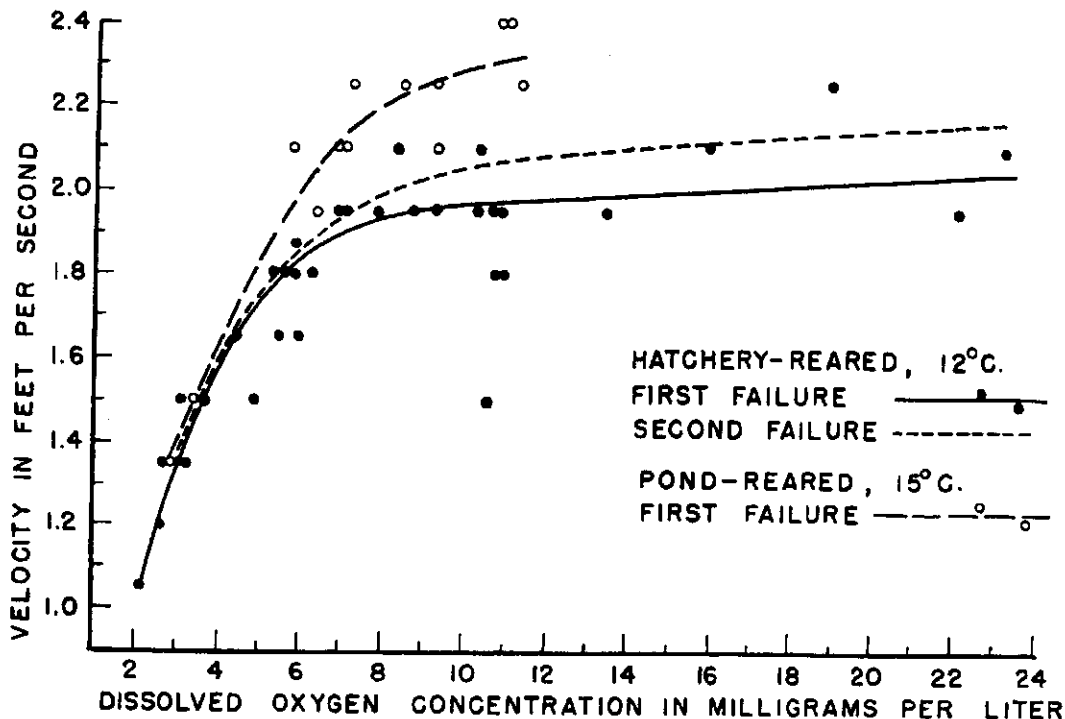


FIGURE 4.—Water velocities at which swimming failures of hatchery-reared and pond-reared yearling coho salmon occurred, in relation to dissolved oxygen concentration. The data or points to which the second-failure curve for hatchery-reared fish was fitted are not shown.

comparable tests. The performance of the pond-reared yearlings was markedly better than that of the hatchery-reared fish at oxygen concentrations above 5 mg/l. The performance of the yearlings, like that of the underyearlings, was evidently impaired by reduction of the dissolved oxygen concentration to levels much below the air-saturation levels.

Curves representing the relations between oxygen concentration and water velocities effecting first failures and second failures of hatchery-reared yearlings are included in Figure 4. Only the points to which the first-failure curve was fitted (solid circles) are shown. The single curve for pond-reared yearlings in Figure 4 is based upon first-failure observations (open circles). Second-failure data were not regularly recorded in the experiment with pond-reared fish; also, owing to the paucity of available material, no tests were performed with these fish at oxygen concentrations above 11.5 mg/l.

Although the swimming performance of the first hatchery-reared yearlings to fail at 12° C.

was markedly impaired at low oxygen concentrations, apparently there was little improvement of the performance of these fish when the oxygen concentration was increased from 7 or 8 mg/l to levels near and well above the air-saturation level (about 10.8 mg/l). The results were highly variable, however, and consequently the fit to these experimental data of the curve in Figure 4 is not good. The curve based on second failures shows considerably more improvement of swimming performance with an increase in oxygen concentration from 7 or 8 mg/l to the air-saturation level than is shown by the otherwise similar curve based on first failures.

The curves in Figure 4 show that, at air-saturation levels of dissolved oxygen, first failures of hatchery-reared and pond-reared yearlings were to be expected at water velocities near 1.95 and 2.3 f.p.s., respectively. At oxygen concentrations below 5 mg/l, the difference in performance of the hatchery-reared and pond-reared fish was not pronounced. The small difference in mean size of the

TABLE 2. — *Percent reduction of the swimming speed of coho salmon at each of several lower levels of dissolved oxygen from the speed at the air-saturation level*

Experimental material and temperature	Percent reduction of swimming speed at dissolved oxygen concentration of:				
	3 mg/l	4 mg/l	5 mg/l	6 mg/l	7 mg/l
Wild underyearlings					
10° C.	33.31*-33.8	19.4 -21.2*	11.9 -13.3*	7.8 - 8.5*	4.4 -5.3*
15° C.	28.1*-29.1	19.7*-20.1	13.5*-13.9	9.3*-10.1	5.8*-6.4
20° C.	26.6*-28.0	16.7*-18.4	9.9*-11.5	5.9*- 7.4	3.2*-4.1
All temperatures	26.6*-33.8	16.7*-21.2*	9.9*-13.9	5.9*-10.1	3.2*-6.4
Yearlings					
Hatchery-reared					
12° C.	31.6 -34.0*	20.8 -23.1*	12.4 -15.0*	7.6 -10.2*	3.8 -5.8*
Pond-reared					
15° C.	38.7	29.1	19.9	12.5	7.0

\* Percent reduction of swimming speed based on second failure. Values not so designated are based on first failures.

the largely laboratory-reared underyearlings tested at temperatures near 15° C. is more nearly rectilinear, within the range of tested oxygen concentrations (about 1.5 to 9 mg/l), than those observed in other experiments with chinook and coho salmon. The conclusion that the performance of the fish probably would have been better at the air-saturation level of dissolved oxygen (about 10 mg/l) than at 9 mg/l, and better yet at a concentration above the air-saturation level, is unavoidable. At these high concentrations, the underyearlings tested at the lower temperatures probably would have been nearly all capable of performance better than the average performance at the same concentrations of the first-failing fish tested at the higher temperatures. The striking difference between the results of the two experiments is not attributable entirely to temperature differences nor to differences in size or age of the fish, and so it must have been due largely to other undetermined factors.

Like the swimming speed of the largely laboratory-reared underyearlings at temperatures near 15° C., the performance of the larger hatchery-reared yearlings tested at lower temperatures, especially those fish that had not been used previously, seemed to decline sharply with decrease of oxygen concentration from the highest tested levels (slightly below the air-saturation level) to 5 or 6 mg/l. However, the further impairment of the performance with a decrease of oxygen concentration from about 5 to 2 or 3 mg/l was greater than that shown by the last-mentioned underyearlings, and much like that shown by the hatchery-reared underyearlings tested at temperatures near 19.5° C. The significance

of the difference between the results of the two series of tests with previously unused and once-used yearlings (Figure 5) is not clear. The previous experience of the once-used fish in the experimental apparatus may have influenced their performance. It should be noted, however, that a few of the least vigorous fish used in the initial series of tests were discarded and not included in the lot of once-used yearlings saved for the succeeding tests, and this may have influenced the test results also.

#### *Comparative results*

Table 2 shows the percent reduction of the swimming speed of coho salmon below the speed at the air-saturation level of dissolved oxygen for each of several arbitrarily selected lower oxygen concentrations. The reduction percentages are based on velocities taken from the curves fitted to the experimental data (Figures 2, 3, and 4). Second-failure as well as first-failure curves were used when available. The computed percent reductions of the swimming speed of coho salmon at each oxygen concentration considered (Table 2) are moderately uniform. Only the relatively high percentages derived from the curve for pond-reared yearlings, which is based on few and rather variable experimental data, are notably different from the corresponding percentages derived from the other curves. The latter values (*i.e.*, exclusive of those for pond-reared yearlings) pertaining to oxygen concentrations of 3, 4, 5, 6, and 7 mg/l average 30.6, 19.9, 12.7, 8.4, and 4.9 percent, respectively. The limited data available indicate that the corresponding percent reductions of the swimming speeds of healthy chinook salmon at 11

tures near 19.5° C. to perform much better at higher oxygen concentrations than at concentrations between 5 and 7 mg/l was due to an abnormally low oxygen capacity of their blood. Unlike the underyearlings tested at lower temperatures (which had been reared mostly at the laboratory, on a diet predominantly of beef liver), these fish had been recently obtained from the hatchery, where a high incidence of anemia among juvenile chinook salmon at other times has been reported. Even at oxygen concentrations well below the air-saturation level, the blood of those individuals that failed first may have been, at the time of their failure, oxygenated virtually to capacity after passing through the gills. Unfortunately, no measurements of the hemoglobin content of the blood of these fish were made.

The observed anemic condition of many of the hatchery-reared coho salmon may have influenced the results obtained with these fish also. The curve based on first failures among these fish (Figure 4) shows some improvement of performance with an increase of oxygen concentration from 8.0 mg/l to levels far above the saturation level. However, this improvement may be unreal, or it may have been exaggerated by sampling errors, for the data to which the curve was fitted are highly variable. The blood hemoglobin of some of the more anemic individuals possibly was oxygenated at the gills nearly to its capacity even when these fish were swimming at their maximal speed at ambient oxygen concentrations below 8 mg/l.

At concentrations at which the swimming performance and active metabolic rate are oxygen-concentration dependent, the rate of oxygen consumption and the performance of fish may be limited by the greatest attainable rate of gill irrigation or respiratory volume (Fry, 1957; Basu, 1959). However, Shepard's (1955) data on the influence of acclimation to reduced oxygen concentrations upon the active rate of oxygen uptake of brook trout, and his seemingly valid interpretation thereof (p. 425), supported by the data of Prosser *et al.* (1957), indicate that the oxygen transport capacity of the blood also may be of some importance. At higher oxygen concen-

trations (*i.e.*, in the zone of independence), the maximum sustained swimming speed of healthy (*i.e.*, not anemic) fish at a given temperature may be determined by their muscular capabilities or by the effectiveness of the existing stimulus. Basu (1959) has suggested that the active oxygen consumption rate at these concentrations is limited by the normal oxygen transport capacity of the blood. Shepard's (1955) findings fail to support this view, for at high oxygen concentrations he detected no significant difference in active oxygen uptake rates of brook trout acclimated to high and low concentrations, but his fish may not have been stimulated sufficiently to evoke maximum rates.

In the experiments reported herein, some of the fish were tested at somewhat unseasonable temperatures markedly higher than those at which they had been held before they were placed in the experimental apparatus. The previous exposure of these fish to lower temperatures, especially the underyearling coho salmon tested at 20°C., may have influenced the test results because of incomplete thermal acclimation (see Fry and Hart, 1948). It should be noted, however, that the 15°C. curves in Figures 2 and 3 are based on tests with wild underyearling cohos that had been held at stream-water temperatures very near the test temperature. Prolonged acclimation of the fish to the various tested oxygen concentrations probably would have altered the results somewhat, increasing the swimming speeds at reduced oxygen concentrations, as it has been shown to influence the active metabolic rates of brook trout (Shepard, 1955).

The improvement of the swimming performance of juvenile coho salmon resulting from temperature increases up to 20°C. reported herein has been observed also by Brett, Hollands, and Alderdice (1958). However the mean cruising speeds, even of yearlings recorded by these authors were considerably lower than the maximum sustained swimming speeds of the weakest (first-failing) wild underyearlings of slightly smaller average size tested at corresponding temperatures and a oxygen concentrations near air-saturation in our studies. Most of the latter fish apparently were able to continue swimming (for 10 min

In waters receiving organic wastes, etc., reduced oxygen concentrations normally are associated with elevated concentrations of free carbon dioxide. Basu (1959) has presented data on the influence of carbon dioxide at different temperatures and oxygen concentrations upon the active metabolic rate and scope for activity of brook trout that had been recently placed in the experimental media. From these data one can infer that the percent reductions of the sustained swimming speed of juvenile salmon at reduced oxygen concentrations perhaps would have been appreciably greater than those observed had an amount of carbon dioxide been added to the water approximately equivalent to the amount of oxygen removed in each test. However, the data of McNeil indicate that the adverse effects of moderate concentrations of carbon dioxide on the tolerance of low oxygen concentrations by resting coho salmon are transient, the fish evidently becoming acclimatized very soon to these carbon dioxide concentrations. The same may well be true of any effects on the active metabolic rate and swimming performance.

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