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The Influence of Oxygen Concentration on the Swimming Performance of Juvenile Pacific Salmon at Various Temperatures[1, 2]

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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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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.[5]

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.

[5] 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.

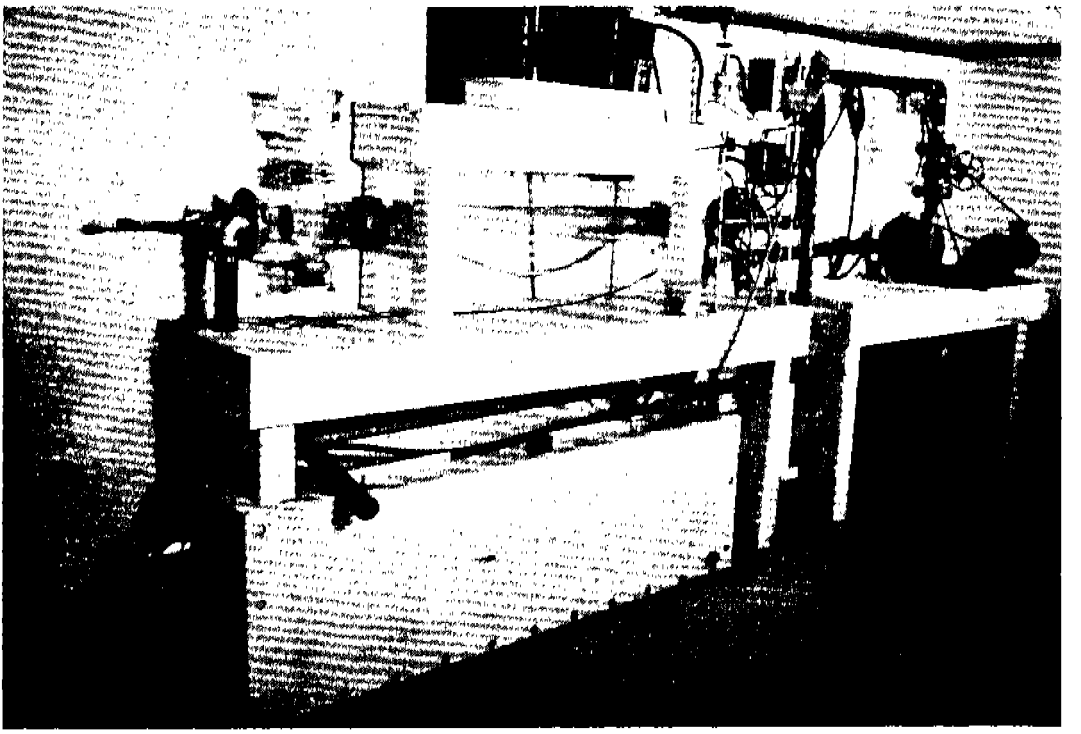

FIGURE 1.—Apparatus used for swimming performance studies. For a detailed semidiagrammatic drawing of the same apparatus see Katz, Pritchard, and Warren (1959).

Losses of fish in the stock tanks usually were insignificant. However, heavy losses of hatchery-reared coho salmon yearlings followed a rise of water temperature in the spring of 1959. Use of the surviving fish was discontinued when it became apparent that many were diseased. All fish were carefully examined at the time of their removal from tanks for use in experiments, and those that were evidently deformed or in poor condition were rejected.

Table 1 shows the age classes, rearing histories, and fork lengths (means and ranges) of coho and chinook salmon tested at different specified temperatures, and also the inclusive dates of each experiment.

Experimental apparatus

The experimental apparatus is pictured in Figure 1. A schematic drawing showing more detail has been presented by Katz, Pritchard, and Warren (1959). The test animals were

TABLE 1.—*Kinds, age classes, rearing histories, and fork lengths of salmon used in experiments at specified temperatures during different periods, listed chronologically*

Inclusive dates of experiment	Species of salmon	Age class (years)	Rearing history	Fork length (millimeters)		Test temperature (° C.)
				Mean	Range	
3/1/58–4/25/58	Chinook	1	Hatchery-reared	96	81–126[1]	11.5
5/14/58–6/13/58	Chinook	0	Lab-reared[2]	59	51–73	15
7/16/58–8/12/58	Chinook	0	Hatchery-reared	68	57–76	10.5
12/5/58–4/18/59	Coho	1	Hatchery-reared	127	112–144	12
6/6/59–6/28/59	Coho	1	Pond-reared	133	127–144	13
7/6/59–9/6/59	Coho	0	Wild stock	77	67–89	15
9/8/59–11/7/59	Coho	0	Wild stock	80	76–88	20
11/12/59–12/31/59	Coho	0	Wild stock	84	79–90	10

[1] The fork lengths of 96 percent of these fish were less than 110 millimeters.
[2] Obtained from hatchery when very young and reared thereafter in laboratory stock tanks.

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° C., but brief failures of the thermoregulatory system resulted in larger fluctuations up to about 2.5° 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 or 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 auto-

matic temperature controls were actuated. The test temperature usually was attained in about 1 hour. The fish were then left undisturbed until the following morning to become accustomed to the experimental conditions. They were able to maintain their position in the tube with little or no exertion. In the morning, usually about 16 hours later, the water velocity was increased by 0.10-f.p.s. increments at 20-minute intervals until a velocity of 0.75 f.p.s. was reached. At this time, the concentration of oxygen in the incoming water was adjusted to the appropriate level. The dissolved oxygen content of the water in the system reached the desired constant level, and the fish learned to swim steadily against the current during a subsequent 3-hour period. The base velocity of 0.75 f.p.s., which was deemed necessary for ensuring sustained activity of all the fish, was uniformly maintained throughout this period. At the end of the 3-hour preparatory period, the water velocity was gradually increased by definite increments until one or two fish failed to continue swimming. The velocities at which the first and second swimming failures occurred were recorded in most of the coho salmon experiments. Only the velocity for the first failure was recorded, however, in tests with chinook and pond-reared yearling coho salmon, which were terminated upon failure of the first fish.

All yearling coho salmon were subjected to velocity increments of 0.15 f.p.s. every 20 minutes. In tests with coho salmon underyearlings, the velocity increments and time intervals were half as great; *i.e.*, 0.075 f.p.s and 10 minutes, respectively, excepting some special tests. The velocities successively tried in experiments with yearling chinook salmon were 0.75, 1.05, 1.27, 1.55, 1.75, and 2.0 f.p.s., and those tried in tests with underyearlings were 0.75, 0.93, 1.05, 1.16, 1.27, 1.35, 1.45, 1.55, 1.63, and 1.75 f.p.s. Velocities were increased every 20 minutes in all tests with chinook salmon.

In experiments with coho salmon, a beam of light from a 60-watt incandescent lamp was directed at the downstream end of the tube to discourage fish from swimming in the immediate vicinity of the perforated closure. The possibility of occasional premature failure of the fish due to accidental impingement on the screen thus presumably was reduced.

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 it occurred was recorded. Upon the failure of one or two fish, a sample of the effluent water from the test chamber was taken for determination of the dissolved oxygen content by the Alsterberg (azide) modification of the Winkler method, and the test was terminated. The fish then were removed from the apparatus and measured, and usually were liberated thereafter. Excepting a few fish that had been evidently injured, yearling chinook salmon used in an initial series of successful or abortive tests were used again in an immediately succeeding series of additional tests. They were held in stock tanks and fed for at least a few days before the second use.

The use of five fish in each test and the observation of first or first and second failures only had their origin in early exploratory experiments. In these experiments, attempts were made to measure median performance using five yearling chinook salmon in each test. Determinations of current velocities causing third failures then yielded highly variable results. It was concluded that two or three of the five fish, probably the more vigorous ones, often were able to take advantage of small eddies in the vicinity of the baffles at the upstream end of the test chamber by occupying favorable positions with relatively low water velocities just downstream from the baffles. The first and second fish to fail apparently had derived little or no benefit from the presence of the eddies, not having found them or having yielded the favorable positions. The third fish to fail presumably had benefited greatly in some of the tests, but not in others. It was noted also that a change of hydraulic conditions within the test chamber could result from the obstruction of perforations of the downstream closure by two or more fish forced against the closure. Yet reduction of the number of fish in a test group to three in order to overcome the latter difficulty in evaluating median performance was not deemed expedi-

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).[6] These values are deemed sufficiently instructive, however, and usable without correction for present comparative purposes.

[6] 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:

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

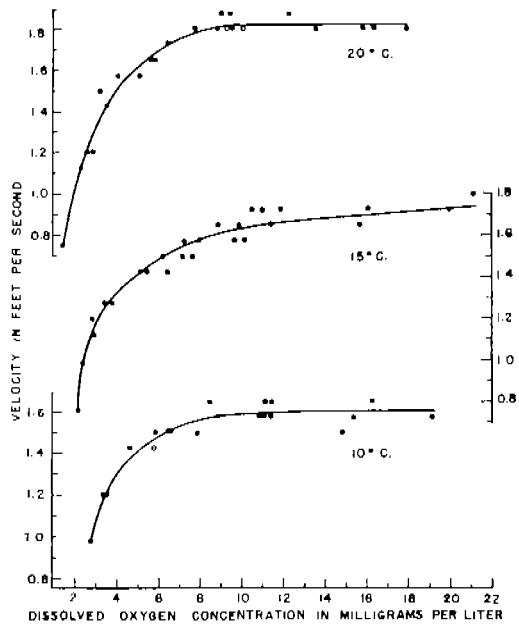

FIGURE 2.—Water velocities at which swimming failures of first-failing wild underyearling coho salmon occurred at 10, 15, and 20° C., in relation to dissolved oxygen concentration.

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-

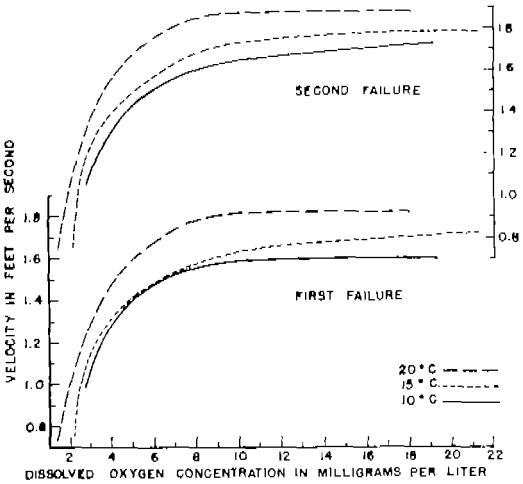

FIGURE 3.—Comparison of curves relating oxygen concentration to swimming performance of first-failing and of second-failing underyearling coho salmon at three different temperatures.

ner are shown as solid circles. The four points plotted as open circles along the 20° C. and 10° C. curves are based on first failures in tests in which the time interval between successive velocity changes was doubled (*i.e.*, increased from 10 to 20 minutes). The proximity of these points to the curves, which were fitted to the solid circles, indicates that the increase of the time interval did not materially influence the test results.

The points representing failures at the base velocity of 0.75 f.p.s. cannot be deemed entirely valid. Each of these failures occurred during the 3-hour period allowed for reducing the oxygen concentration to the desired (ultimate) constant level, which had been nearly attained at the time when the failure occurred. At that dissolved oxygen level the failure conceivably could have occurred also at a water velocity somewhat less than the chosen base velocity.

The deviations of the experimental data from the three curves shown in Figure 2 are not great. At all three test temperatures, the velocities at which first failures occurred declined markedly when the oxygen concentration was reduced to levels much below 9 or 10 mg/l. They increased little or none with an increase of oxygen concentration beyond this level, which is not far from the air-saturation level for each test temperature. The air-saturation values at 10, 15, and 20° C. have been reported to be about 11.3, 10.2, and 9.2 mg/l dissolved oxygen, respectively (American Public Health Association, 1960).

The deviations of the second-failure data from hand-drawn curves fitted by eye apparently were no greater than were those of the first-failure data. Figure 3 permits comparison of the curves based on first and second failures of underyearling coho salmon at the three different temperatures. In each set of three curves, the 20° C. curve is positioned well above the essentially similar 10° C. curve, the performance of the fish at any oxygen concentration being evidently better at the higher temperature than at the lower temperature. The expected intermediate position of the 15° C. curve is best seen in the second-failure series. The differences in shape of the six curves appear to be largely fortuitous and ascribable to experimental or sampling errors.

Blood samples for hemoglobin determination were taken from 10 recently captured, wild, underyearling coho salmon, and from 10 that had been held in the stock tanks at the laboratory for almost 4 months. The hemoglobin values obtained averaged 11.5 g/100 ml and ranged from 9.6 to 13.5 g/100 ml. The mean values for the recently collected fish and for those that had been held at the laboratory for a long time were 11.9 and 11.1 g/100 ml, and the standard deviations were 1.1 and 1.0, respectively. The small difference between the means is not statistically significant. Although the samples were small, it can be concluded that no serious alteration of the hemoglobin content of the blood of the fish resulted from their captivity. The uniformity of results obtained with fish held at the laboratory for varying periods of time, which is indicated by the good fit of the data to the plotted curves, also shows that holding the fish at the laboratory resulted in no serious deterioration of their physical condition.

Yearling coho salmon

The swimming speeds of the yearling coho salmon at temperatures near 12° and 15° C. (Figure 4) understandably proved greater than those of the smaller underyearlings in

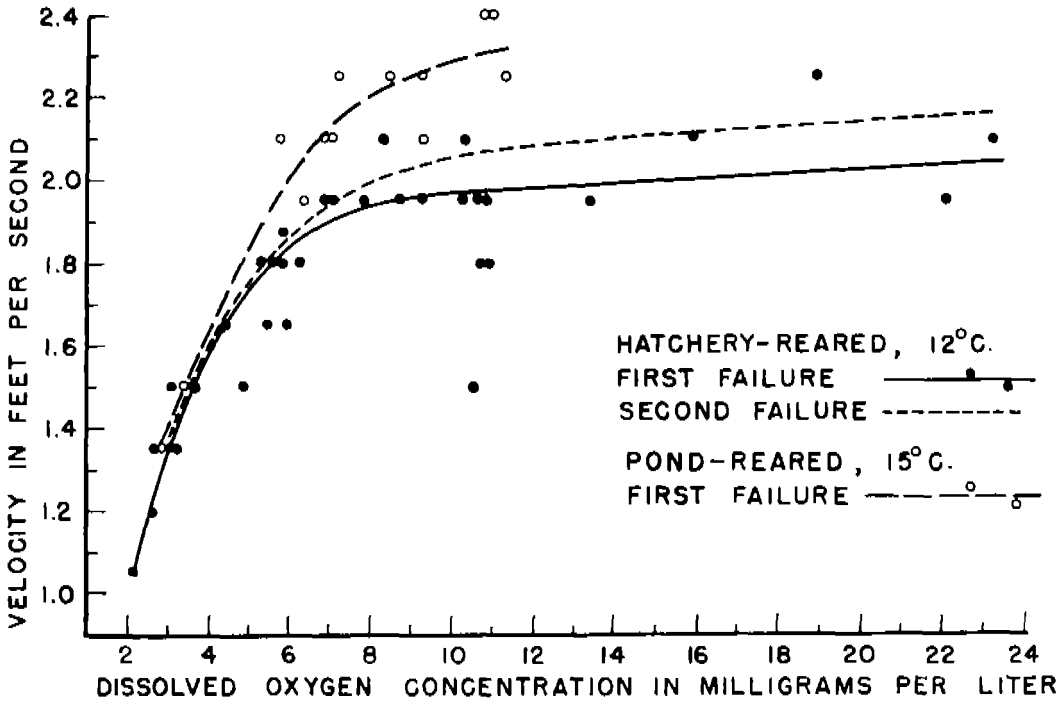

FIGURE 4.—Water velocities at which swimming failures of hatchery-reared and pond-reared yearling coho salmon occurred, in relation to dissolved oxygen concentration. The data or points to which the second-failure curve for hatchery-reared fish was fitted are not shown.

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

hatchery-reared and pond-reared fish and the difference of temperatures at which their swimming ability was tested may have contributed to the observed difference of their performance. However, the difference in performance probably is ascribable chiefly to a difference in physical condition of the two groups of fish. The range of blood hemoglobin values determined for a sample of 39 fish taken from the hatchery-reared stock was 4.8 to 12.9 g/100 ml. The mean and the standard deviation were 9.5 and 2.3 g/100 ml, respectively. A sample of 32 fish taken from the pond-reared stock yielded values ranging from 8.7 to 15.3 g/100 ml. The mean and the standard deviation were 11.9 and 1.6 g/100 ml, respectively. The difference between the means for the two samples is highly significant statistically. The great variability of the hemoglobin content of the blood of the hatchery-reared yearlings may have been at least partly responsible for the large variability and generally low level of the performance of early-failing individuals in different tests at oxygen concentrations above 5 mg/l.

Chinook salmon

The number of observations made in the course of each of several experiments with chinook salmon was relatively small, and the comparable results of individual tests were rather variable, perhaps partly because of minor variations of procedure which had not yet been refined and fully standardized when the chinook salmon experiments were undertaken. For these reasons, the analysis and interpretation of the results of these exploratory experiments cannot be carried far. The results are sufficiently interesting, however, to be reported briefly.

Two experiments with underyearling chinook salmon at temperatures near 15 and 19.5° C. yielded strikingly unlike results (Figure 5). The swimming performance of the first-failing fish at the higher test temperatures appeared to be virtually independent of oxygen concentration when the concentration was above 7 mg/l. The results obtained at the lower temperatures indicated that the performance probably was dependent on oxygen concentration not only throughout the range

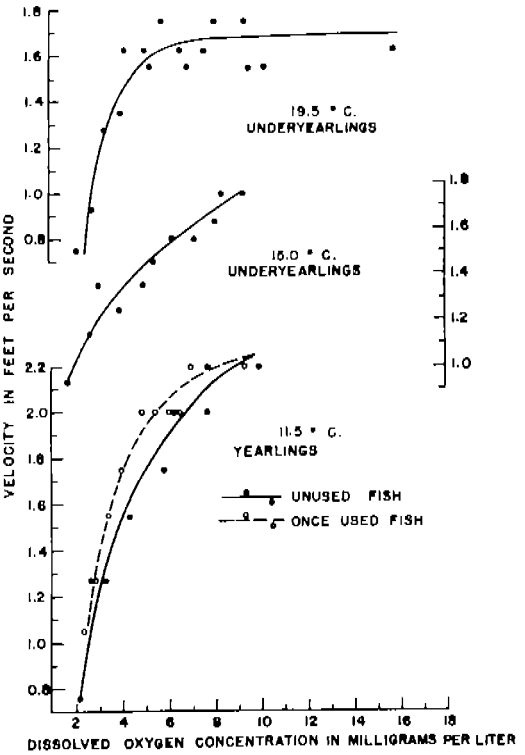

FIGURE 5.—Water velocities at which swimming failures of first-failing yearling and underyearling chinook salmon occurred at different temperatures, in relation to dissolved oxygen concentration.

of tested concentration (up to about 9 mg/l), but also at higher concentrations. The results of earlier tests at low temperatures (near 11.5° C.) with yearling chinook salmon (Figure 5) had suggested a relationship between oxygen concentration and swimming performance somewhat intermediate in nature between those indicated by the results of the two experiments with underyearlings.

The observations and curves plotted in Figure 5 pertain to first failures only, data on second failures of chinook salmon not having been regularly recorded. The performance of first-failing hatchery-reared underyearlings at temperatures near 19.5° C. improved greatly with an increase of oxygen concentration from about 2 to 5 mg/l, but there is no indication that an increase beyond 7 mg/l had any favorable influence on the performance. The relation between oxygen concentration and swimming speed observed in the experiment with

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.	33.3*–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

to 15° C. may be decidedly greater; namely, about 38, 27, 20, 14, and 10 percent, respectively. These values are not markedly different from those estimated for the pond-reared yearling coho salmon (Table 2).

DISCUSSION

It has been shown that the sustained swimming performance capability of coho and chinook salmon usually is impaired when the dissolved oxygen concentration is reduced from the air-saturation level to any considerably lower level, but at much higher concentrations the performance of coho salmon improves only slightly, or not at all. Graham (1949) found that the cruising speed of brook trout at 8° C. was appreciably reduced only when the oxygen concentration was lowered to levels below 6 mg/l (about 50 percent of air-saturation). The data of Ferguson reported by Fry (1957) indicate, however, that the cruising speed of the yellow perch is reduced somewhat at oxygen concentrations only a little below the air-saturation level, especially at the higher test temperatures. Unlike the curves presented in this paper, curves relating the cruising speed of the perch to oxygen concentration, except one obtained at the lowest test temperature of 10° C., show an abrupt change in slope at an oxygen concentration near 3 mg/l. The performance of the perch was greatly impaired only at oxygen concentrations below this level.

The results of experiments with brook trout reported by Graham (1949) and experiments with lake trout, *Salvelinus namaycush* (Walbaum), reported by Gibson and Fry (1954) indicated that the active metabolic rates, or maximum rates of oxygen uptake (Fry, 1957), of these salmonids generally are dependent on oxygen concentration only at concentration levels considerably below the air-saturation levels. However, Graham's finding was not confirmed by Job (1955) and Basu (1959), who found the active oxygen consumption rates of the brook trout to be dependent on oxygen concentrations up to, or even well above, the air-saturation levels, except at very low temperatures. Basu stimulated the fish by means of an electric barrier, whereas Graham, Gibson and Fry, and Job did not.

The relation between metabolic rate and swimming performance capability has been discussed by Fry (1947, 1957). He presented evidence that cruising speed increases as the square root of the "metabolic difference" or "scope for activity" (*i.e.*, the active rate less the standard rate) increases. From this it can be inferred that determinations of active or maximum steady rates of oxygen consumption perhaps can demonstrate a potential for slight improvement of sustained swimming performance at increased oxygen concentrations that cannot be readily demonstrated by measurement of the performance itself. It can be concluded also that the moderate increases of active oxygen uptake rates that were observed by Job (1955) when oxygen concentrations were raised beyond the air-saturation levels probably indicate only very small increases of sustained swimming speed. However, the relation between the rates of oxygen uptake and actual steady swimming speeds of a fish in a rotating annular respirometer is not simple and well established. Basu (1959), in his Table II (p. 183), and Fry[7] have reported that the oxygen uptake rates of brook trout and carp that had been recently placed in a respirometer increased little or none with threefold to sixfold increases of respirometer rotation rates (beyond 5 or 6 revolutions per minute). Yet, Basu also reported large increases of the oxygen uptake rate of trout resulting from mild electrical stimulation without increase of the respirometer rotation rate (*i.e.*, at each rate tested). This indicates that in the absence of such stimulation the oxygen uptake rates at all the swimming speeds were much less than the highest possible rates. The significance of the metabolic rate data needs further clarification before these data can be properly compared with and related to independently obtained swimming performance data.

It has been noted that strikingly dissimilar results were obtained in different experiments with chinook salmon (Figure 5). It seems reasonable to suppose that the inability of the first-failing underyearlings tested at tempera-

[7] Personal communication and unpublished account of recent experimental results obtained by D. W. Coble, received from Dr. F. E. J. Fry in July 1961.

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 concentrations (*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 at oxygen concentrations near air-saturation in our studies. Most of the latter fish apparently were able to continue swimming (for 10 min-

utes) at speeds only slightly (about 0.1 f.p.s.) below 1.60, 1.65, and 1.80 f.p.s. at temperatures of 10, 15, and 20° C., respectively (Figure 2). Second-failing fish (Figure 3) and average individuals usually were able to maintain even greater speeds. The cruising speeds (maintained for 1 hour or longer under strong stimulus) of yearlings tested at the same temperatures by Brett, Hollands, and Alderdice averaged only 1.16, 1.23, and 1.35 f.p.s., respectively. The fish used by them had been hatched, reared, and thermally acclimated at the laboratory, and they were tested in a rotating annular trough. The dissimilarity of results probably is ascribable mostly to differences of the material, apparatus, and methods employed, and not to unavoidable errors in the evaluation of absolute swimming speeds due to inequality of water velocities at different points in a test chamber, etc.

Unlike the results of prolonged tests at moderate water velocities reported by Katz, Pritchard, and Warren (1959), the data presented in this paper and those of Brett, Hollands, and Alderdice have application where high levels of sustained activity may be required of juvenile salmon for relatively short periods of time. The relation between swimming time and the highest water velocity resisted by these fish has not yet been thoroughly investigated. However, instructive results were obtained from the few tests at 10 and 20° C. wherein underyearling coho salmon were required to resist each successively tested velocity above the base velocity of 0.75 f.p.s. for a period twice the normal time interval between velocity increments (open circles in Figure 2). From these results one can conclude that the maximum sustained swimming speed of which an individual is capable is not a function of swimming duration within time limits as yet undefined. Although seemingly not in agreement with Boyar's (1961) data on the swimming performance of young Atlantic herring, this conclusion is supported by the data of Brett, Hollands, and Alderdice. They found that, after an initial period of swimming "bursts" and "slumps," which usually could be prevented by gradually increasing the rate of trough rotation in the course of about 1 hour, juvenile coho salmon would continue swimming at a nearly constant maximum sustained or cruising speed for an hour or much longer before fatigue set in. Yet, the fish certainly are capable of much more rapid swimming for very short periods of time.

Situations wherein the survival of juvenile salmon could depend on sustained rapid swimming are readily imaginable, but whether or not such swimming at speeds approaching the measured maxima is necessary in the course of normal feeding and migratory activities is not known. Also, it is not known whether or not the ability of the fish to perform brief bursts of intense activity, such as may be necessary to avoid capture by predators, would be influenced by reduction of oxygen concentration as was their sustained swimming ability in the reported tests. This question and the influence of dissolved oxygen on the resistance of the fish to fatigue when swimming for long periods at various speeds short of the highest possible sustained or cruising speeds still need investigation.

At the present time, one can only speculate about the ecological significance of the observed impairment of performance at oxygen concentrations not far below the air-saturation levels. One can reasonably argue that fish are not likely to possess performance capabilities that do not contribute to their success or well-being in nature. In accordance with this view, Fry (1957) stated that "Any reduction of the oxygen content below the level where the active metabolic rate begins to be restricted is probably unfavorable to the species concerned." Apparently there is no evidence, however, to support this view, and perhaps a different view also can be effectively defended. Certainly one can reasonably argue that some slight restriction of the maximum sustained swimming speed of salmon, through reduction of dissolved oxygen in portions of streams receiving organic wastes, probably would not usually result in serious damage to salmon populations. In this connection, the rather large variation in performance capacity of coho salmon with normal variations of temperature (Brett, Hollands, and Alderdice, 1958), and the observed differences between individuals of about the same size or age, should be noted.

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[8] 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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