AN ABSTRACT OF THE THESIS OF

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Title: Influence of Oxygen Concentration and of its Diurnal Fluctuations on the Growth of Juvenile Coho Salmon

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Three laboratory experiments were performed to determine the influence of constant, nonlethal dissolved oxygen concentrations, both above and below the air-saturation level, and also of wide diurnal fluctuations of dissolved oxygen concentration on the growth, food consumption, and food conversion efficiency of underyearling coho salmon, Oncorhynchus kisutch (Walbaum).

The experimental apparatus used in this study was designed to provide a constant flow of water of controlled temperature and dissolved oxygen concentration through seven test vessels, each containing 15 fish. The test temperature was 18° C. The desired oxygen concentrations were maintained by bubbling nitrogen, air or oxygen through the inflowing water. The fish were fed mainly tubificid worms.

The growth rates of fish exposed for 18 days in two experiments

to constant oxygen concentrations (ranging from 3.0 to 29.9 mg./l., and from 2.5 to 35.5 mg./l.) and kept on an unrestricted diet decreased markedly with decrease of oxygen concentration from the air-saturation level (9.5 mg./l.). Oxygen concentrations about twice the air-saturation value had a slightly favorable influence on growth, while concentrations more than three times the air-saturation level slightly depressed the growth rates. The differences of the growth rates observed at different oxygen concentrations were associated with corresponding differences of food consumption rates. Food conversion efficiencies of fish held at different constant oxygen concentrations were not markedly different, there having been no appreciable impairment of the efficiency at concentrations as low as 3.8 mg./l.

The fish kept on an unrestricted diet grew fairly rapidly and showed greater percent gains in crude fat than in body weight (wet or dry), and consequently greater percent gains in dry weight than in wet weight, even at reduced oxygen concentrations as low as 2.5 and 3.0 mg./l. At each concentration tested the fat deposited in the tissues accounted for nearly one-third of the total dry weight gain.

The growth of fish exposed daily for equal periods to non-lethal low and high dissolved oxygen levels, in the course of the above two experiments, was more or less impaired. In the first experiment, the growth of these fish was little better than that of fish exposed continuously to the low level of dissolved oxygen to which the fish subjected to fluctuations of dissolved oxygen

were exposed only intermittently. In the second experiment, the intermittent exposure to a very low oxygen concentration reduced the growth rate less markedly. Very wide fluctuations of oxygen concentration between two higher levels, levels that did not prove markedly unfavorable for growth in tests at constant concentrations, had even less depressing effect on growth.

The growth rates of fish kept for 21 days on equal, restricted rations at various constant oxygen concentrations ranging from about 3.0 to 18.1 mg./l. did not differ greatly; only the growth of the fish exposed to the lowest tested dissolved oxygen level showed considerable impairment, ascribable to impaired digestive or assimilatory efficiency. The gross food conversion efficiencies of all the fish in this experiment proved markedly greater than those of the fish that had been fed unrestricted rations under the same conditions in the earlier experiments, although the growth rates of the former fish were much less than those of the fish fed unrestricted rations.

INFLUENCE OF OXYGEN CONCENTRATION AND OF ITS DIURNAL FLUCTUATIONS ON THE GROWTH OF JUVENILE COHO SALMON

by

RICHARD JOSEPH FISHER

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Professor of Fisheries

In Charge of Major

Redacted for privacy

Head of Department of Fish and Game Management

Redacted for privacy

Dean of Graduate School

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INTRODUCTION

A laboratory investigation was conducted from May through July 1962, to determine the influence of dissolved oxygen concentration on the growth of juvenile coho salmon, Oncorhynchus kisutch (Walbaum). Two experiments were designed to determine the effects of different, nearly constant oxygen concentrations and also of diurnal fluctuations of oxygen concentration upon the growth, food consumption, and food conversion efficiency of juvenile coho salmon kept on an unrestricted diet. A third experiment was designed to determine the effects of different, nearly constant oxygen concentrations on the growth and food conversion efficiency of juvenile coho salmon kept on a uniform, restricted diet. These experiments were performed at Oregon State University's Oak Creek Laboratory, located near Corvallis.

Some waters, especially those receiving putrescible organic wastes such as municipal sewage, have more or less reduced oxygen concentrations which, even when not low enough to be lethal to fish, may seriously interfere with their growth. Lethal oxygen levels are uncommon in fish habitats, whereas persistent nonlethal, low oxygen concentrations and diurnal fluctuations of oxygen concentrations are encountered frequently. The dissolved oxygen content of waters enriched with organic wastes is reduced through oxidative decomposition of the organic matter by bacteria, and the products of decomposition are utilized as nutrients by algae and thus can cause algal "blooms". Because of the photosynthetic activity of

algae and other aquatic plants, the dissolved oxygen concentration may rise to very high levels during the day. At night, the oxygen concentration may drop to critically low levels due to respiratory consumption of oxygen by algae and other aquatic organisms, and bacterial action on the remaining organic matter. Tarzwell and Gaufin (12, p. 300) reported that in Lytle Creek, a small stream in Ohio polluted with municipal sewage, the oxygen concentration varied from 19.4 milligrams per liter in the afternoon to 0.7 mg./l. the following morning. Oxygen concentrations as high as 27.6 and 32.1 mg./l. have been reported in ponds and lakes (14, p. 126) (16, p. 115).

According to Stewart (10, p. 4), Haempel (8, p. 553-570) found that water supersaturated with dissolved oxygen can be harmful and fatal to fish. However, other investigators have found that different fishes can tolerate very high oxygen concentrations for prolonged periods of time. Wiebe and McGavock (15, p. 267-274) found that various centrarchids, salmonids, and cyprinids were able to withstand long exposures to oxygen concentrations ranging from two to more than three times the air-saturation level. Food consumption and growth rates of the fish were not determined by these investigators.

The ability of fishes to survive at low oxygen concentrations for short periods of time has been frequently studied. Doudoroff (6, p. 403-430), Tarzwell (11, p. 246-272), Townsend and Earnest

(13, p. 345-351), and Davison et al. (5, p. 950-966) have adequately summarized the results of these studies. Doudoroff (6, p. 413-415) points out that the cold-water salmonids, whose dissolved oxygen requirements have been frequently studied, are among the fresh-water fishes that are most sensitive to the reduction of dissolved oxygen.

The effects of less extreme oxygen concentrations, both below and above the air-saturation level, on the growth, food consumption, and food conversion efficiency of fish have not been as frequently studied. Doudoroff (6, p. 413-415) and Davison et al. (5, p. 950-951) have pointed out the lack of information concerning the effects of reduced oxygen concentrations on the general well-being and performance of fish. Stewart (10, p. 3) has discussed the need for information concerning the influence of dissolved oxygen concentrations well above the air-saturation level and of wide diurnal fluctuations of oxygen concentration, as well as of low concentrations, on the growth, food consumption, and food conversion efficiency of fish.

Davison et al. (5, p. 950-966) determined the growth and food consumption rates of yearling coho salmon, kept at 18° C. on a uniform, restricted diet at oxygen concentrations near air-saturation and below. At oxygen concentrations averaging 2 mg./l., the fish consumed very little of the food offered and lost weight. At oxygen concentrations averaging 2.9 and 9 mg./l., the fish consumed nearly all of the food offered and showed 28.1 and 43

percent gains in wet weight, respectively. As noted by the authors, the difference in weight gain may have been partly or entirely attributable to the fact that the fish tested at 9 mg./l. were somewhat smaller at the beginning of the experiment than those tested at 2.9 mg./l., so that an effect of the low oxygen concentration on food conversion efficiency was not conclusively demonstrated.

Herrmann, Warren, and Doudoroff (9, p. 155-167) found that juvenile coho salmon kept at 20° C. at constant oxygen concentrations near and below the air-saturation level and fed beach hoppers (marine amphipods) to repletion, their growth, food consumption, and food conversion efficiency were markedly influenced by oxygen concentration. Their results indicated that the food consumption and growth rates tended to decrease somewhat with reduction of dissolved oxygen concentration from about 8.3 to 6 and 5 mg./l., and to decline more markedly with further reduction of oxygen concentration. The gross food conversion efficiencies were virtually unaffected by reduction of oxygen concentration to 4 mg./l., but the efficiencies were markedly reduced at lower concentrations. The reduction of gross conversion efficiency may have been ascribable entirely to the markedly reduced food consumption rates of the fish held at the very low oxygen concentrations, but some inconclusive evidence was presented that digestive or assimilatory efficiency also may have been impaired. The effects of constant oxygen concentrations above the air-saturation level, and of diurnal fluctuations of oxygen

concentration on the growth, food consumption, and food conversion efficiency of coho salmon were not determined by these investigators.

Stewart (10, p. 16-31) found that the growth and food consumption of juvenile largemouth bass, Micropterus salmoides (Lacépède), kept at 26° C. and at constant oxygen concentrations on an unrestricted diet of earthworms, increased markedly as oxygen concentrations increased to levels near the air-saturation level. Further increase of the oxygen concentration, beyond the air-saturation level, resulted in a decrease in growth and food consumption rates. Stewart found that food conversion efficiencies of bass at the various tested oxygen concentrations above 4 mg./l. did not differ markedly, but below 4 mg./l., the efficiencies were considerably reduced. Stewart also exposed bass each day to low and higher dissolved oxygen concentrations. He found that the growth and appetite of these bass were markedly impaired in each such test. The food consumption and growth rates of these fish were less than the rates which presumably would have occurred had the fish been held at constant concentration equal to the mean (either the arithmetic or the geometric mean) of the low and the high concentrations to which the fish had been alternately exposed.

One purpose of the present investigation was to re-evaluate the influence of different constant, nonlethal oxygen concentrations below the air-saturation level on the growth, food consumption, and food conversion efficiency of coho salmon, through experiments similar to those of Herrmann, Warren and Doudoroff (9, p. 155-167),

but keeping the fish on a different unrestricted diet and at a somewhat lower (and presumably more favorable) temperature. Attention has been given not only to gains in wet weight of the fish, but also to gains in dry weight and to changes in the crude fat content and calorific value of the dry material. Another purpose of the study was to determine whether or not supersaturation of water with oxygen and wide diurnal fluctuations of oxygen concentration have adverse effects on the growth of coho salmon similar to those observed by Stewart (10, p. 16-31) in his experiments with largemouth bass. A third purpose was to compare the food conversion efficiencies of coho salmon kept at different constant oxygen concentrations on a restricted diet, and thus to detect any important adverse effect of reduced or abnormally high oxygen concentrations on the efficiency of digestion or assimilation of food by the fish.

EXPERIMENTAL MATERIAL, APPARATUS, AND METHODS

Experimental Material

The coho salmon fingerlings used in the first experiment were hatched and reared at the Oak Creek Laboratory from eggs that were obtained from a single female in October 1962, at the United States Fish and Wildlife Service's Eagle Creek Hatchery, located on Eagle Creek, a tributary of the Clackamas River in northern Oregon. These fingerlings were reared in an outdoor wooden trough until they were

of the desired size. The mean total length of the fish used in the first experiment (no. 1) was 50.9 millimeters.

The coho salmon fingerlings used in the second and third experiments were seined on June 1 and June 29, 1962, from the upper Yaquina River in Lincoln County, Oregon. The mean total lengths of the fish used in the second and third experiments (nos. 2 and 3) were 51.2 and 53.4 millimeters, respectively.

Experimental Apparatus

The experimental apparatus used in this study provided a constant flow of water of controlled temperature and dissolved oxygen concentration to seven test vessels containing the test fish. The apparatus was located in a constant-temperature room illuminated with fluorescent lights. The apparatus is pictured in Figure 1. Figure 2 is a schematic drawing showing in detail only one of the seven identical units of which the experimental apparatus is comprised.

A detailed description of the design and functioning of an experimental apparatus similar to that used in this study is given by Davison *et al.* (5, p. 951-954); later modifications thereof have been described by Stewart (10, p. 5-8), whose apparatus was used in this study. Therefore, only a general description of the apparatus used will be given in this report.

Filtered water from a spring-fed stream, supplied to the laboratory through polyethylene pipe, was introduced into an overflowing five-gallon constant-head jar of Pyrex glass. From this

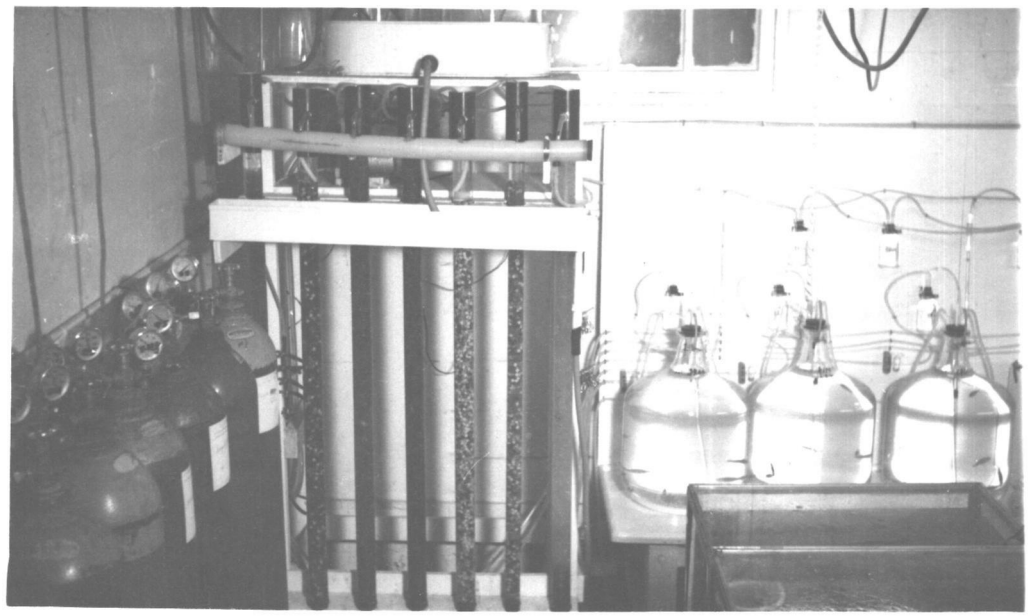

Figure 1. Two views of the experimental apparatus.

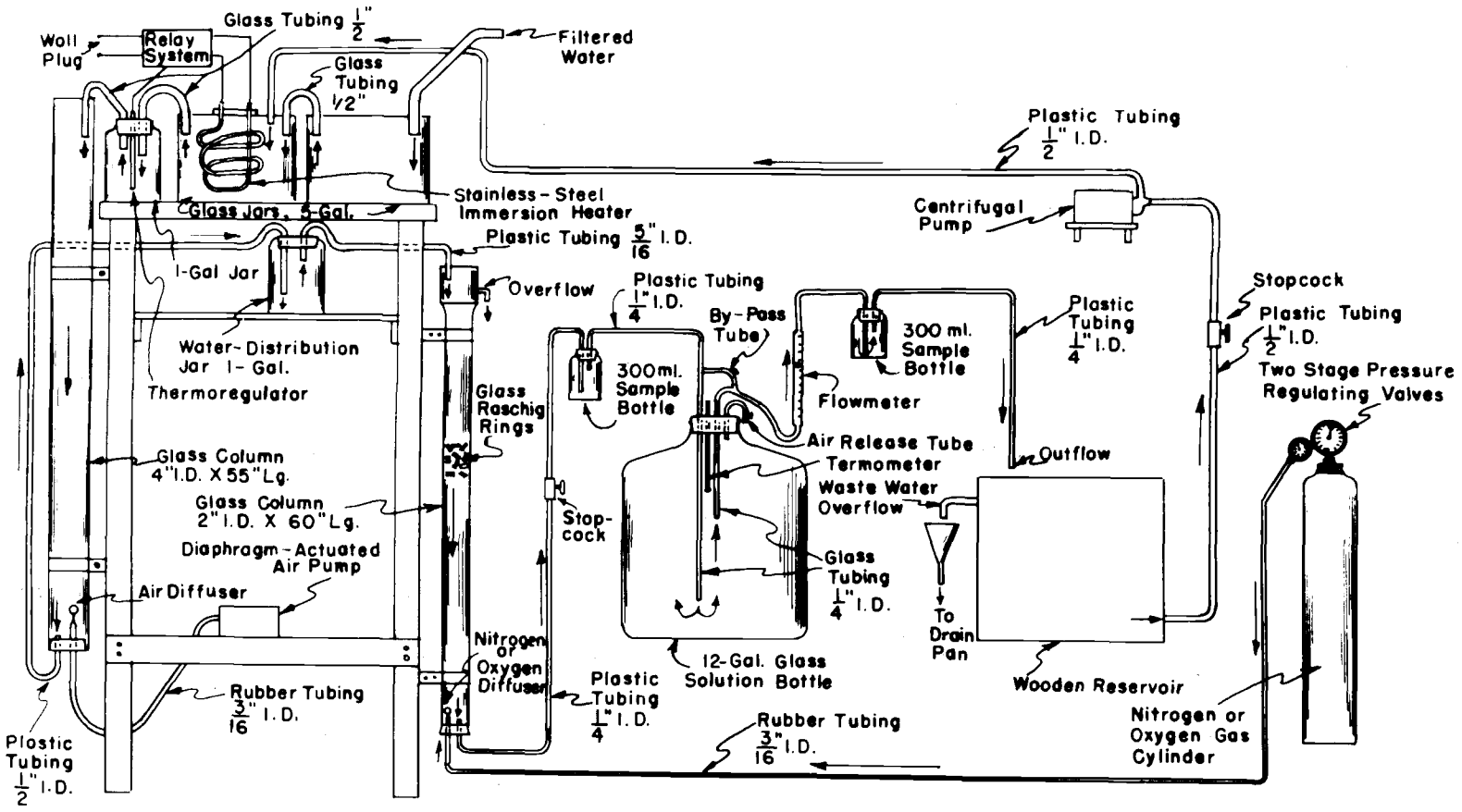

Figure 2. Schematic drawing of the experimental apparatus. One of seven units is shown.

jar, the water was siphoned into a similar jar where it was heated to the desired temperature by a thermostatically controlled, stainless steel immersion heater. The heated water then flowed through a one-gallon jar containing a mercury thermoregulator and into the top of a large glass column. A large quantity of finely dispersed air was continually introduced at the bottom of the column. This was done to bring the dissolved oxygen content of the water to near the air-saturation level. The aerated water flowed from the bottom of the column through a distribution jar and to the tops of seven glass columns filled with Raschig rings. As the water flowed downward in each column, its dissolved oxygen concentration was adjusted to the desired level by means of a controlled counterflow of compressed air, nitrogen, or oxygen introduced at the bottom of the column. After leaving the glass column at the bottom, the water flowed through a flow-adjustment stopcock and a 300-milliliter sampling bottle into a 12-gallon Pyrex glass bottle which held the test fish. From this test vessel, the water flowed through a ball-displacement flowmeter, through another 300-milliliter sampling bottle, and into a wooden reservoir.

Water was discharged into the wooden reservoir at a rate of approximately 500 milliliters per minute from each of the seven test vessels. About 65 percent of this discharged water was returned by a small centrifugal pump to the jar containing the immersion heater. This was necessary to conserve heat in maintaining a constant water temperature. The remaining 35 percent of the water

flowed out of the reservoir through an overflow tube and was discarded. Fish excrement and other debris settled to the bottom of the reservoir and were periodically removed.

Experimental Methods

Eight to ten days before the start of an experiment, about 200 fingerlings were placed in a 50-gallon glass aquarium, where they were acclimated to a water temperature of about 18° C. Tubificids were the principal food provided the fingerlings during the acclimation period. Supplementary feedings with commercially prepared dry food and live cladocerans were made occasionally. Fish that appeared unhealthy or failed to eat during this period were removed from the aquarium and discarded.

The experimental apparatus was placed into operation 24 hours before the start of an experiment to stabilize the water temperature at 18° C. and test the gear. The dissolved oxygen concentration of the water in all the test vessels was maintained at a level near the air-saturation level until soon after the introduction of the test fish, when the dissolved oxygen concentrations were adjusted to the desired test levels. About five hours were required for completion of this adjustment. Lights in the laboratory room were controlled by a timing device so as to come on at 6:00 a.m. and to go off at 10:00 p.m.

One hundred twenty fish of approximately equal size were removed from the acclimation aquarium and divided into eight groups

of 15 fish each. All groups were of nearly equal weights. Seven of these groups were placed into the seven test vessels after having been blotted with cleansing tissue and weighed in water. The fish of the eighth group were anesthetized with MS 222 (tricane methanesulphonate), individually weighed and measured, and dried in an oven at 70° C. The crude fat content and calorific value of this sample were determined by procedures to be described later.

In order to maintain the desired experimental conditions, it was necessary to check the operation of the experimental apparatus twice each day and make any needed adjustments. The first daily check in all experiments was made between 8:00 and 9:00 a.m. The second check was made between 8:00 and 9:00 p.m. in experiments 1 and 2, and between 4:00 and 5:00 p.m. in experiment 3. During these check periods, the temperature and water flows were measured and recorded, and the dissolved oxygen concentrations of the water entering and leaving each of the test vessels were determined. The Alsterberg (azide) modification of the Winkler method (1, p. 309-312) was used to determine all dissolved oxygen concentrations with the exception of those exceeding 14 mg./l., which were determined by the Pomeroy-Kirschman-Alsterberg method (1, p. 316-317).

In experiments 1 and 2, in which the effects of fluctuating as well as constant dissolved oxygen concentrations were studied, the fish in two of the test vessels were subjected to a low level and then a high level of dissolved oxygen for equal periods each day. The oxygen content of the incoming water was reduced at 9:00 p.m.

and increased at 9:00 a.m. The time required for the oxygen concentration to reach the desired constant level after each of these adjustments was approximately five hours.

Food was introduced into the test vessels between 9:00 and 10:00 a.m., after removing, by siphoning, excrement that had settled to the bottoms. Care was taken during the cleaning process not to remove any food that remained from previous feedings. Tubificids and a relatively small quantity of cladocerans were used as food for the fish in experiments 1 and 2, while the fish in experiment 3 were fed tubificids only. The tubificids fed during the experiments were held in fresh water without food for at least 24 hours to minimize their weight changes due to loss of intestinal contents. Before the tubificids were fed to the fish they were placed on paper towels for about two minutes to remove most of the adhering water and then weighed. At intervals throughout experiments 2 and 3, samples of the tubificids were weighed before and after drying at 70° C. The mean "percent dry weight" of the samples of food (i.e., dry weight expressed as a percentage of the wet weight) was determined and used in computing the dry weight of the food consumed by the test fish in each vessel.

In experiment 1, the fish were fed an unrestricted diet of food in amount to more than they could consume, and only the type of food introduced (tubificids or cladocerans) was recorded. The diet and feeding procedure in experiment 2 were the same as in experiment 1, except that the food introduced daily into each test vessel was

weighed and an attempt was made to introduce such an amount of food that only a small excess would remain in each vessel at the end of each 24-hour period between feedings. In experiment 3, the fish in each of six test vessels each day were fed a restricted diet of tubificids in amount equal to the amount consumed over a 15-minute period on the same day by the fish in the seventh test vessel, which were subjected to the lowest dissolved oxygen concentration tested. The food was introduced into the last-mentioned (seventh) test vessel in small amounts during the daily 15-minute feeding period, taking care to insure that the amount of food not immediately consumed would not exceed the amount that would be consumed before the next daily feeding.

At the termination of each experiment the oxygen concentrations were returned to near the saturation level in all test vessels. The fish were then held without food for about 24 hours, after which the fish were removed and individually weighed and measured. The fish were then dried at 70° C. for at least five days and the dry weight, calorific value, and crude fat content of each group were determined.

A Parr oxygen bomb calorimeter (No. 1411) and appropriate, standard calorimetry and computation methods were used to determine the calorific values of samples of dried fish. Each group of dried fish, including the initial sample of 15 fish taken at the beginning of each experiment, was ground into fine particles with a mortar and pestle from which pellets weighing 0.1 to 0.3 grams were formed and burned in the calorimeter. At least two calorimetric

determinations were made on each group of fish, including the initial sample, from the results of which the mean calorific value of the dry material was computed.

A Goldfisch continuous ether-flow extraction apparatus was used to determine the crude fat content of the dried fish. The crude fat was extracted with ethyl ether from a one- to two-gram sample of each group of finely ground fish, including the initial sample, and the percentage of crude fat in the dry material was determined.

RESULTS

The three experiments reported herein were conducted from May through July, 1962. The experimental conditions are shown in Table 1. The results of the experiments are shown in Tables 1, 2, and 3.

Table 1 shows the inclusive dates and duration of each experiment, the oxygen concentrations (means and ranges) in each test vessel for each experiment, and the temperatures (means and ranges) of the water in four of the seven test vessels. Also, the mean initial and final wet and dry weights and total lengths of the fish tested at each oxygen concentration are shown. The initial and final dates shown for each experiment are, respectively, the date of the first feeding and the date of the last feeding, which is also the date of removal from the test vessels of any uneaten food remaining from the last feeding. The initial dry weight shown for each group of fish used in each experiment is based on the wet weight of the group and the

Table 1. Experimental Conditions and Mean Weights and Lengths of Fish

Experiment Number and Test Period	Dissolved Oxygen (mg/l) Mean	Dissolved Oxygen (mg/l) Range[1]	Temperature (°C) Mean	Temperature (°C) Range[1]	Mean Weight of Fish (g) Wet Initial	Mean Weight of Fish (g) Wet Final	Mean Weight of Fish (g) Dry Initial[2]	Mean Weight of Fish (g) Dry Final	Mean Total Length of Fish (mm) Initial[3]	Mean Total Length of Fish (mm) Final
Experiment 1	3.0	2.6– 3.8	—	—	1.39	2.90	0.282	0.669	51.6	67.1
5/15–6/2/62	5.3	4.9– 5.9	—	—	1.31	3.84	0.266	0.918	50.7	72.7
18 days	9.5	8.8–10.6	18.4	18.0–19.5	1.29	4.07	0.263	0.982	50.5	74.2
	17.7	16.3–18.9	18.4	18.0–19.8	1.30	4.18	0.263	1.021	50.6	74.7
	29.9	27.2–31.4	18.5	18.0–19.8	1.38	4.23	0.279	1.016	51.5	74.5
	3.0– 9.5[4]	2.7–10.2	—	—	1.35	3.15	0.273	0.733	51.2	68.4
	3.0–18.0[4]	2.4–19.0	18.4	17.8–19.7	1.27	3.17	0.258	0.736	50.2	68.7
Experiment 2	2.5[5]	2.0– 3.4	—	—	1.21	2.01	0.233	0.451	52.9	59.0
6/12–6/30/62			—	—	(1.13)	—	(0.217)	—	(52.0)	—
18 days	3.8	2.8– 4.5	18.2	15.2–19.5	1.16	2.38	0.223	0.555	52.3	62.1
	5.9	4.9– 7.4	—	—	0.97	2.19	0.186	0.507	49.9	60.9
	9.7	9.2–11.1	18.4	15.9–20.0	1.08	2.64	0.209	0.643	51.3	64.2
	35.5	31.4–36.9	18.2	15.0–19.5	0.99	2.27	0.191	0.538	50.2	61.5
	2.3– 9.6[4]	2.2–10.2	—	—	1.02	2.21	0.196	0.515	50.6	60.9
	4.9–35.5[4]	4.0–36.3	18.2	16.6–19.6	1.12	2.60	0.215	0.628	51.8	63.3

(Continued)

Table 1. Continued

Experiment Number and Test Period	Dissolved Oxygen (mg/l) Mean	Dissolved Oxygen (mg/l) Range 1/	Temperature (°C) Mean	Temperature (°C) Range 1/	Mean Weight of Fish (g) Wet Initial	Mean Weight of Fish (g) Wet Final	Mean Weight of Fish (g) Dry Initial 2/	Mean Weight of Fish (g) Dry Final	Mean Total Length of Fish (mm) Initial 3/	Mean Total Length of Fish (mm) Final
Experiment 3	3.0	2.6- 3.4	18.9	18.0-21.0	1.27	2.37	0.246	0.551	52.9	60.1
7/6-7/27/62	3.06/	2.7- 3.4	18.7	17.9-20.0	1.28	2.39	0.247	0.541	53.0	60.4
21 days	4.0	3.5- 4.3	—	—	1.34	2.52	0.258	0.588	53.6	61.5
	5.3	4.7- 5.6	18.7	18.1-20.8	1.32	2.47	0.254	0.580	53.4	61.2
	7.0	6.3- 7.6	—	—	1.34	2.51	0.258	0.589	53.6	61.8
	9.4	8.3-10.2	—	—	1.35	2.46	0.261	0.575	53.8	61.2
	18.1	17.0-19.0	18.6	17.8-21.0	1.31	2.52	0.251	0.585	53.3	61.5

1/ Range of observed values only.

2/ The mean initial dry weight was derived from the wet weight by using a factor (ratio of dry weight to wet weight) determined from a sample of 15 fish taken at the beginning of each experiment.

3/ The mean initial length was derived from a length-weight regression according to the line determined from a sample of 15 fish taken at the beginning of each experiment.

4/ The fish were subjected for equal periods each day to oxygen concentrations near the lower and upper of the two values shown (mean low and mean high concentration extremes).

5/ Due either to a miscount in the number of fish to be placed in the test vessel, or to the subsequent loss of one fish (most likely at the test's conclusion), two sets of values are given for the test at this concentration. The upper values were computed on the basis of 14 fish (the more probable number) having been present throughout the test; the lower values, in parentheses, were computed on the basis of the assumption that 15 fish had been present and one was lost at the end of the test.

6/ One fish died from food strangulation four days after the experiment began.

ratio of dry weight to wet weight of the initial sample of 15 fish taken at the beginning of the experiment. The dry weights of the initial samples in experiments 1, 2, and 3 were found to be equal to 0.203, 0.193, and 0.193 times their wet weights, respectively. The mean initial dry weight for each group of fish was determined by multiplying the wet weight of the group by the appropriate decimal fraction and dividing the product by the numbers of fish in the group. The mean initial length shown for each group of fish was derived from the mean wet weight, using a length-weight regression line determined by weighing and measuring individually the 15 fish taken as a sample at the beginning of the experiment.

At the termination of experiment 2, the number of fish in the group held at 2.5 mg./l. dissolved oxygen was observed to be one less than the expected fifteen. It is deemed most probable that the fish were miscounted at the beginning of the experiment. Evidence supporting this supposition will be presented later. Another possibility is that one fish escaped through a siphon tube at the termination of the experiment. There are also other possibilities, such as the loss of one fish after weighing of the group but before its introduction into the test vessel or soon thereafter (i.e., during feeding), but these are deemed least likely possibilities. For these reasons, two sets of values representing possible results of the one test at 2.5 mg./l. dissolved oxygen appear in Table 1, and also in Tables 2 and 3. The values of one set were computed on

the basis of the assumption that only 14 fish were initially weighed and present in the test vessel throughout the test; the values of the second set (enclosed in parentheses) were computed on the basis of the assumption that 15 fish were tested, but one was lost at the termination of the experiment. The same or intermediate values would have been obtained had computations been made on the basis of any other reasonable assumption. Only the first (upper) set of values is considered and used hereafter (e.g., in presenting the results graphically), except where the relative merits of the stated alternative assumptions are discussed.

Table 2 shows, for each group of experimental fish, the gains per fish in wet and dry weights, in weights of crude fat and of fat-free dry matter (i.e., total dry matter minus the crude fat), and in total "calorific value". These gains are reported in grams or kilocalories and also as percentages of the initial values. The gain per fish in "calorific value" for each group of experimental fish is the difference between mean initial and final values computed by multiplying the initial and final calorific values or caloric equivalents of one gram of dry material (kilocalories per gram of dry fish) by the corresponding (initial and final) mean dry weights of the fish in grams. The initial calorific value per gram of dry material was based on a determination of this value for the sample of fish taken at the beginning of the experiment. The initial calorific values for the fish in experiments 1, 2, and 3 were 5.27, 5.14, and 4.98 kilocalories per gram of dry material,

Table 2. Growth of Coho Salmon at Various Dissolved Oxygen Concentrations

Experiment Number	Mean Oxygen Concentration	Gain per Fish: Wet Weight Grams	Wet Weight Percent	Dry Weight Grams	Dry Weight Percent	Crude Fat Grams	Crude Fat Percent	Fat-free Dry Matter[1] Grams	Fat-free Dry Matter[1] Percent	Calorific Value Kilocalories	Calorific Value Percent
1	3.0	1.51	108	0.387	137	0.120	286	0.267	111	2.346	158
	5.3	2.53	193	0.652	245	0.198	495	0.454	201	3.885	277
	9.5	2.77	214	0.719	274	0.219	558	0.500	224	4.351	314
	17.7	2.88	221	0.758	288	0.227	576	0.531	237	4.538	327
	29.9	2.85	207	0.737	264	0.221	534	0.516	217	4.499	306
	3.0- 9.5[2]	1.80	134	0.460	169	0.144	354	0.316	136	2.712	189
	3.0-18.0[2]	1.90	149	0.478	185	0.143	369	0.335	153	2.894	213
2	2.5[3]	0.80	66	0.218	94	0.067	239	0.152	75	1.133	111
		(0.87)	(78)	(0.234)	(108)	(0.068)	(252)	(0.166)	(87)	(1.409)	(126)
	3.8	1.22	105	0.331	148	0.101	368	0.231	118	2.024	176
	5.9	1.22	127	0.321	172	0.095	421	0.225	138	1.933	202
	9.7	1.55	143	0.433	207	0.139	547	0.295	160	2.648	246
	35.5	1.28	130	0.347	182	0.115	491	0.233	139	2.158	220
	2.3- 9.6[2]	1.19	117	0.319	163	0.097	405	0.221	129	1.940	193
	4.9-35.5[2]	1.48	133	0.413	192	0.131	490	0.282	149	2.512	227

(Continued)

Table 2. Continued

Experiment Number	Mean Oxygen Concentration	Gain per Fish: Wet Weight Grams	Wet Weight Percent	Dry Weight Grams	Dry Weight Percent	Crude Fat Grams	Crude Fat Percent	Fat-free Dry Matter 1/ Grams	Fat-free Dry Matter 1/ Percent	Calorific Value Kilocalories	Calorific Value Percent
3	3.0	1.10	86	0.305	124	0.087	220	0.218	106	1.883	154
	3.0 4/	1.11	87	0.295	120	0.085	218	0.210	101	1.823	149
	4.0	1.18	88	0.330	128	0.096	236	0.234	108	2.039	159
	5.3	1.16	88	0.326	128	0.091	223	0.235	110	1.995	158
	7.0	1.17	88	0.331	128	0.097	238	0.234	108	2.034	158
	9.4	1.11	92	0.314	120	0.092	223	0.222	101	1.931	149
	18.1	1.21	93	0.333	133	0.095	237	0.239	113	2.044	163

1/ The fat-free dry matter values were determined by subtracting the weight of extracted crude fat from the total dry weight.

2/ See footnote 4 in Table 1.

3/ See footnote 5 in Table 1.

4/ The initial weight of the dead fish (see footnote 6 in Table 1) was assumed to be equal to the mean initial weight of all fish. The validity of this assumption is questionable.

respectively, and the corresponding crude fat values were 0.59, 0.36, and 0.59 grams of crude fat per gram of dry material respectively.

Table 3 shows, for each group of experimental fish in experiments 2 and 3, the amounts of food consumed by the fish and the food conversion ratios. The wet and dry weights of food consumed per fish were obtained by dividing the total amounts (wet and dry weights) of food consumed in each test vessel by the number of fish in each test vessel. Inasmuch as one fish died in one test vessel during the course of experiment 3, the amounts of food consumed after the death of this fish by the 14 remaining fish had to be multiplied by 15/14, the product added to the amount of food consumed before the death, and the resulting sum divided by 15 to obtain the total food consumption per fish. Also shown in Table 3 are the wet and dry weights (in grams) of food consumed per day per gram of initial weight of the fish, wet and dry (i.e., wet weight of food consumed per gram of initial wet weight of the fish, and dry weight of food consumed per gram of initial dry weight of the fish). The dry weight of food consumed was computed from the wet weight and was based on the determined ratio of wet weights to dry weights of food samples taken periodically throughout the experiments. The mean dry weight of the tubificid worms was found to be 20.5 percent of the mean wet weight during experiment 2, and 19.3 percent of the wet weight during experiment 3. The mean dry

Table 3. Food Consumption and Conversion by Coho Salmon

Experiment Number	Mean Oxygen Concentration	Weight of Food Consumed per Fish (g)		Weight of Food Consumed per Day Per Gram Initial Fish Weight (g) 1/		Food Conversion Ratio 2/	
		Wet	Dry	Wet	Dry	Wet Weight	Dry Weight
2	2.5 4/	6.00 (5.60)	1.026 (0.958)	0.275 (0.275)	0.245 (0.245)	0.133 (0.157)	0.212 (0.244)
	3.8	7.80	1.421	0.373	0.353	0.156	0.232
	5.9	8.04	1.452	0.460	0.424	0.152	0.221
	9.7	9.99	1.840	0.514	0.486	0.155	0.234
	35.5	8.33	1.525	0.467	0.444	0.154	0.230
	2.3- 9.6 3/	7.99	1.448	0.435	0.403	0.149	0.221
	4.9-35.5 3/	9.06	1.642	0.449	0.434	0.163	0.250
3	3.0	4.87	0.939	0.183	0.182	0.226	0.319
	3.0 5/	4.87	0.939	0.181	0.180	0.228	0.309
	4.0	4.87	0.939	0.173	0.173	0.242	0.351
	5.3	4.87	0.939	0.176	0.176	0.238	0.340

(Continued)

Table 3. Continued

Experiment Number	Mean Oxygen Concentration	Weight of Food Consumed per Fish (g) Wet	Weight of Food Consumed per Fish (g) Dry	Weight of Food Consumed per Day Per Gram Initial Fish Weight (g) 1/ Wet	Weight of Food Consumed per Day Per Gram Initial Fish Weight (g) 1/ Dry	Food Conversion Ratio 2/ Wet Weight	Food Conversion Ratio 2/ Dry Weight
3 (continued)	7.0	4.87	0.939	0.173	0.173	0.240	0.351
	9.4	4.87	0.939	0.172	0.172	0.228	0.330
	18.1	4.87	0.939	0.177	0.178	0.248	0.351

1/ Values in the wet and dry weight columns were based on the wet and dry weights of both fish and food, respectively.

2/ Weight gain per fish in grams divided by the total weight in grams of food consumed per fish. See also footnote 1.

3/ See footnote 4 in Table 1.

4/ See footnote 5 in Table 1.

5/ See footnote 4 in Table 2.

weight of cladocerans used as food in experiment 2 was 8.4 percent of the mean wet weight. The food conversion ratios shown in Table 3 were obtained by dividing the weight gains per fish by the weights of food consumed per fish during the entire experimental period, using the wet weights of both the fish and food and the dry weights of both fish and food.

Growth, Food Consumption, and Food Conversion with Unrestricted Diet

The growth and food consumption rates of fish kept on an unrestricted diet and exposed to either constant or fluctuating oxygen concentrations in experiments 1 and 2 differed markedly, depending upon the experimental conditions to which the fish were exposed. Observed differences in food conversion efficiencies were small.

Figures 3 and 4 show, for fish held at constant oxygen concentrations in experiments 1 and 2, respectively, the percent gains in wet weight, dry weight, crude fat, fat-free dry matter, and calorific value, plotted against the oxygen concentrations at which the fish were tested. These percent gains all decreased curvilinearly with decrease of oxygen concentration from the air-saturation level (9.5 mg./l.). No sharp inflection of the curves that have been fitted, by eye, to the data in Figures 3 and 4 is apparent at any oxygen concentration below the air-saturation level. High oxygen concentrations, except those very far above the air-saturation level, had no adverse effect on growth, concentrations up to about twice the air-saturation level evidently having a slightly favorable

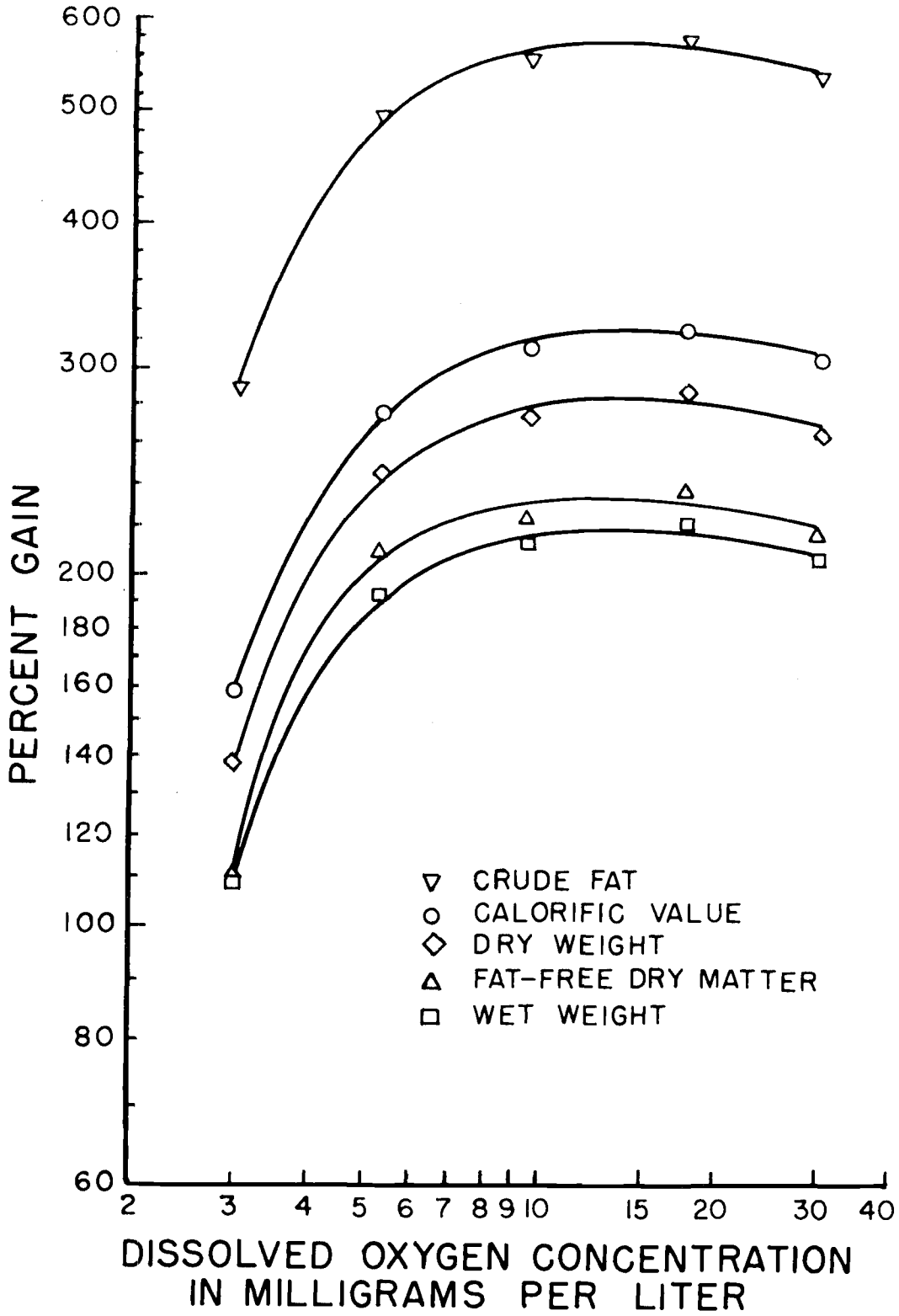

Figure 3. Percent gains, in relation to constant oxygen concentrations, experiment I.

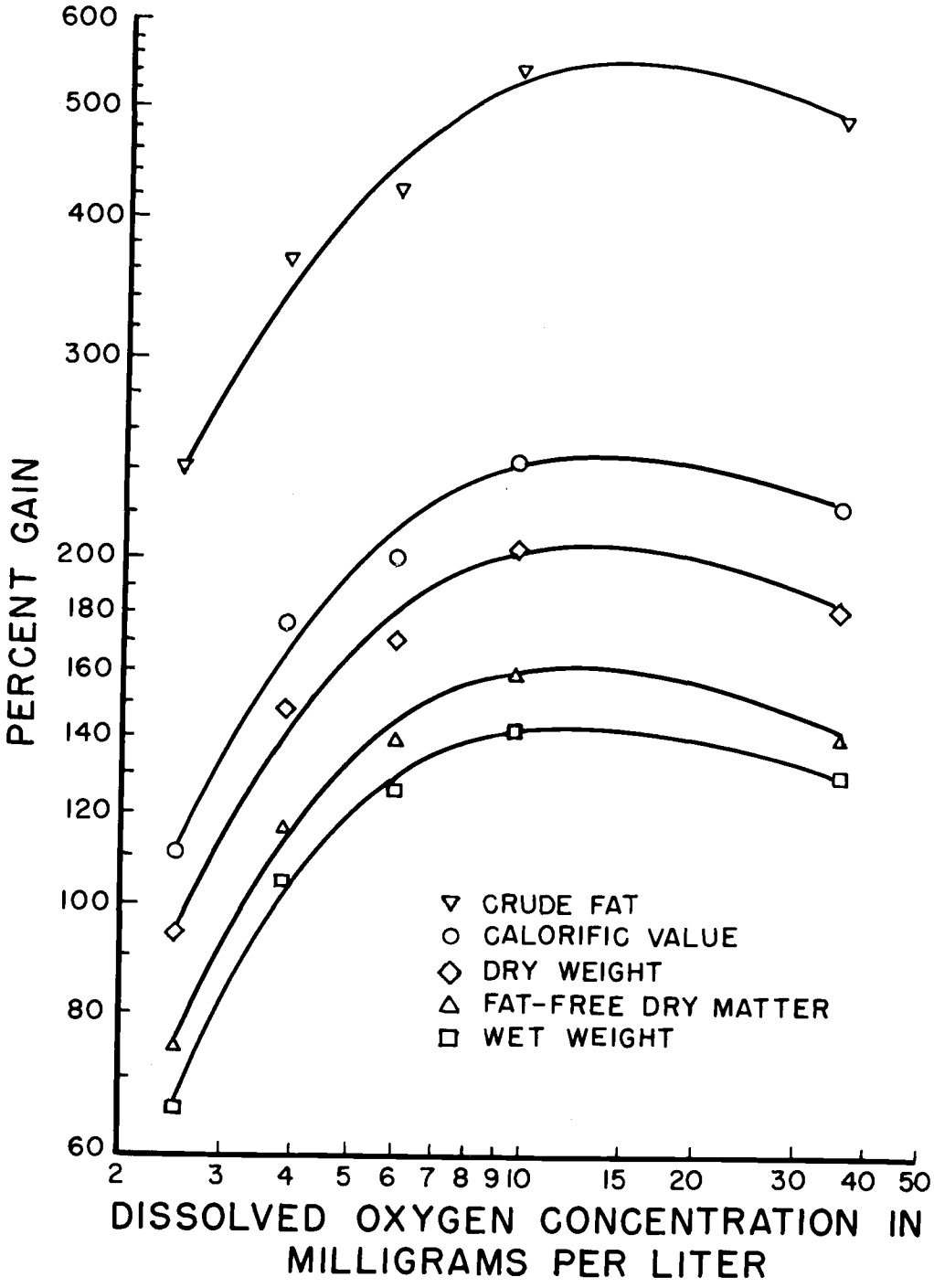

Figure 4. Percent gains, in relation to constant oxygen concentrations, experiment 2.

influence. The adverse effect even of concentrations more than three times the air-saturation level was not very pronounced.

Figures 3 and 4 show that fish tested at all concentrations in experiments 1 and 2 grew at fairly rapid rates. All the fish showed greater gains in crude fat than in body weight (wet or dry), and consequently a greater percent gain in dry weight than in wet weight. Accordingly, the percent gains in calorific value also are relatively great. The percent gains in fat-free dry matter are little different from the percent gains in wet weight.

The absolute gains in dry weight, crude fat, and fat-free dry matter per fish at the various constant oxygen concentrations in experiments 1 and 2 are shown in Figures 5 and 6, respectively. At each concentration tested, the fat deposited in the tissues accounted for nearly one-third of the total dry weight gained per fish. The fraction of the total dry weight gain that is attributable to storage of fat did not decrease markedly with reduction of oxygen concentration and with the accompanying reduction in growth rate. The much poorer fit to the eye-fitted curves in Figure 6 than in Figure 5 of all the data obtained at the oxygen concentration of 5.9 mg./l. is clearly ascribable to the relatively small mean initial weight of the fish tested at this concentration. Not only the points in Figure 6 representing these data, but also all those representing results of the test at the highest constant oxygen concentration, 35.5 mg./l., are unduly depressed in relation to the rest, for the

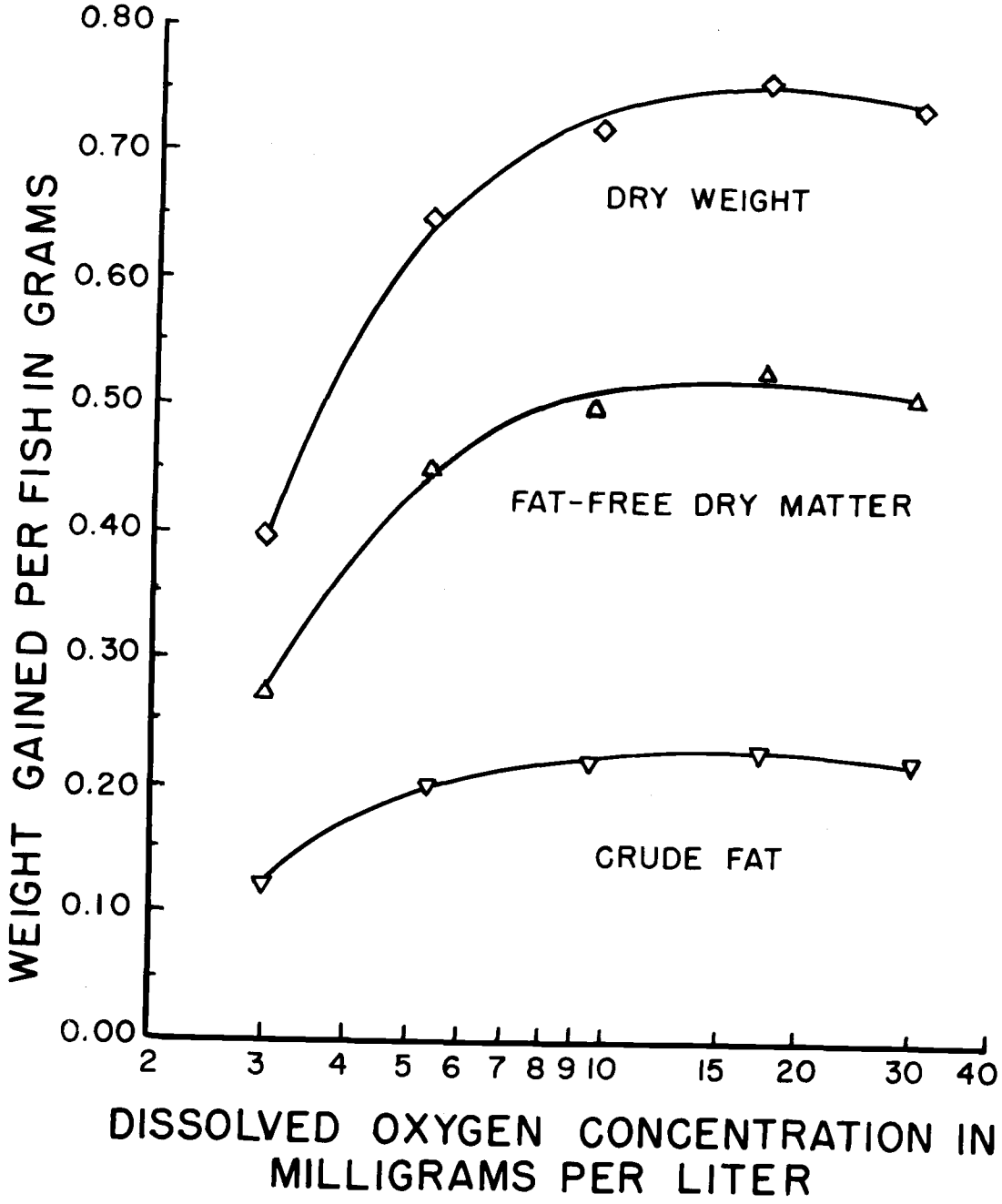

Figure 5. Weight gains per fish in grams, in relation to constant oxygen concentrations, experiment 1.

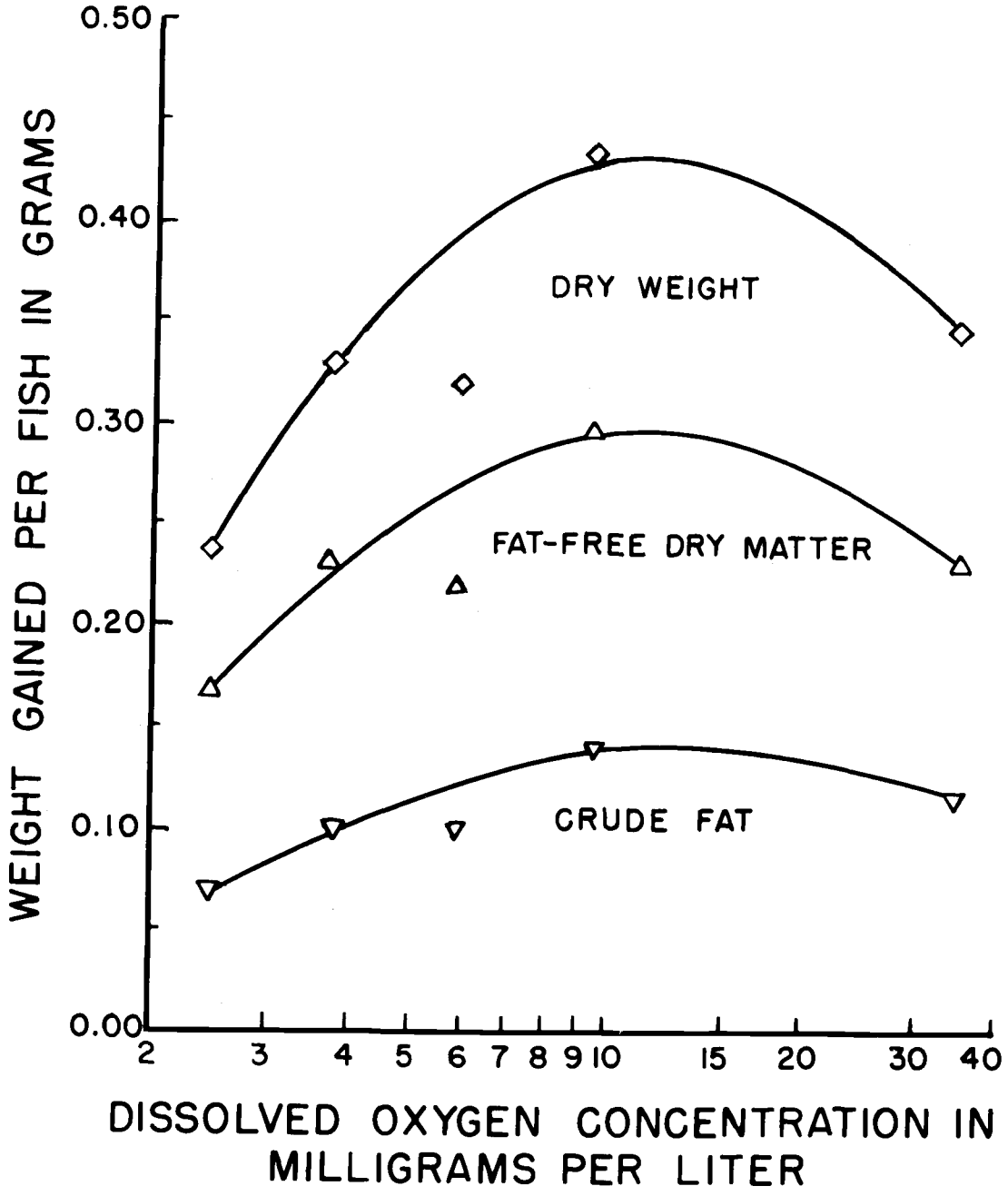

Figure 6. Weight gains per fish in grams, in relation to constant oxygen concentrations, experiment 2.

same reason (i.e., the relatively small initial size of the fish used in the test). The adverse influence of the highest oxygen concentration thus is clearly exaggerated in Figure 6 (see Figure 4).

Figure 7 shows that in experiment 2 the fish did not grow as rapidly as did fish held at about the same oxygen concentrations in experiment 1. The reason for the difference is unknown.

Table 3 summarizes the data from experiment 2 on the food consumption rates of fish kept on an unrestricted diet (mainly of tubificids). The data indicate that food consumption varied with oxygen concentration in much the same way as did the observed gains in weight. The observed differences in the weights gained by the fish at different oxygen concentrations are clearly associated with differences in food consumption.

Table 3 also shows, for experiment 2, the relation between the oxygen concentrations, both constant and fluctuating, and food conversion ratios, or gross conversion efficiencies (3, p. 386). The indicated efficiencies of food conversion by fish held at different constant oxygen concentrations are not markedly different. Of the two possible wet-weight and dry-weight food conversion ratios computed for the lowest concentration (2.5 mg./l.) and shown in Table 3, the smaller (superior) values, namely, 0.133 and 0.212, respectively, are the values that were more in accord with expectations based on the relatively low food consumption and growth rates of the fish in question and on all other available and pertinent

data. The alternative values shown, (0.157 and 0.244), appear to be much too high, supporting the earlier proposed assumption that only 14 fish had been weighed and placed in the test vessel with the lowest oxygen concentration.

The growth rates of fish in experiments 1 and 2 were more or less impaired, as shown in Table 2, by wide diurnal fluctuations of oxygen concentration such that the fish were exposed daily for equal periods to nonlethal low and high oxygen levels. Four different fluctuating dissolved oxygen regimes were tested.

Table 4 shows, for each of the fluctuating oxygen concentration regimes tested in experiments 1 and 2, the mean low and mean high dissolved oxygen concentrations observed, the actual gain in dry weight of the fish, and the estimated constant oxygen concentration at which the observed percent dry weight gain presumably would have occurred had the fish been held at that oxygen concentration. The constant oxygen concentrations corresponding to the fluctuating concentrations in their effect on growth were determined graphically by referring to appropriate curves that relate dry weight gains to constant oxygen concentrations (Figure 7), that is, by interpolation. Also shown on Table 4 are the approximate arithmetic and geometric means of the fluctuating concentrations, and the estimated percent gains in dry weight that presumably would have occurred had fish been held at constant oxygen concentrations equal to the arithmetic and geometric mean concentrations. The estimated gains in dry weight at the arithmetic and geometric mean concentrations were derived

Table 4. Comparison of Dry Weight Gains of Coho Salmon Subjected to Fluctuating Dissolved Oxygen Concentrations with the Gains (Estimated) at Constant Oxygen Concentrations Corresponding to the Means for the Fluctuating Dissolved Oxygen Tests.

Experiment Number	Approximate (Mean) Limits of Dissolved Oxygen Fluctuations (mg./l.)1/		Observed Gain in Dry Weight (Percent)	Corresponding (Estimated) Constant Oxygen Concentration (mg./l.) 2/	Approximate Mean Dissolved Oxygen Concentration (mg./l.)3/		Estimated Gain in Dry Weight (Percent)4/ at Constant Oxygen Concentrations Equal to:	
	Mean Low D.O.	Mean High D.O.			Arithmetic Mean	Geometric Mean	Arithmetic Mean D.O.	Geometric Mean D.O.
1	3.0	9.5	169	3.4	6.2	5.3	253	240
	3.0	18.0	185	3.8	10.5	7.2	281	265
2	2.3	9.6	163	4.8	5.9	4.7	182	163
	4.9	35.5	192	6.8	20.2	13.1	203	209

1/ See footnote 4 in Table 1.

2/ The oxygen concentration at which the observed percent gain in dry weight presumably would have occurred had the fish been held at that constant oxygen concentration.

3/ Arithmetic and geometric means of the mean low and mean high concentrations given in preceding columns.

4/ Weight gain estimates were derived from the appropriate curves in Figure 6.

graphically from the dry weight curves in Figure 7.

In Figure 7, the points indicated by arrows marked A, B, C, and D represent the percent gains in dry and wet weights of the groups of fish tested at fluctuating oxygen concentrations and show their relation to the weight gains observed at different constant oxygen concentrations. The graphical, interpolative estimation of constant oxygen concentration reductions that should have the same effect on growth as did the oxygen concentration fluctuations in question (Table 4), thus is illustrated by Figure 7.

The growth of fish exposed to fluctuating oxygen concentrations in experiment 1 was markedly impaired. Table 4 shows that, at oxygen concentrations fluctuating between 3 and 9.5 mg./l. and between 3 and 18 mg./l., the observed dry weight gains were about 169 and 185 percent, respectively. These observed gains are much less than the gains that could have been expected at constant oxygen concentrations near the arithmetic or geometric means of the fluctuating concentrations tested, and they are gains that presumably would have occurred at much lower constant oxygen concentrations of 3.4 to 3.8 mg./l.

In experiment 2, the percent gains in dry weight of fish exposed to oxygen concentrations fluctuating between 2.3 and 9.6 mg./l. and between 4.9 and 35.5 mg./l. were not greatly different from the dry weight gains that presumably would have occurred had the fish been exposed to constant oxygen concentrations equal to the respective geometric means of the fluctuating concentrations (Table 4).

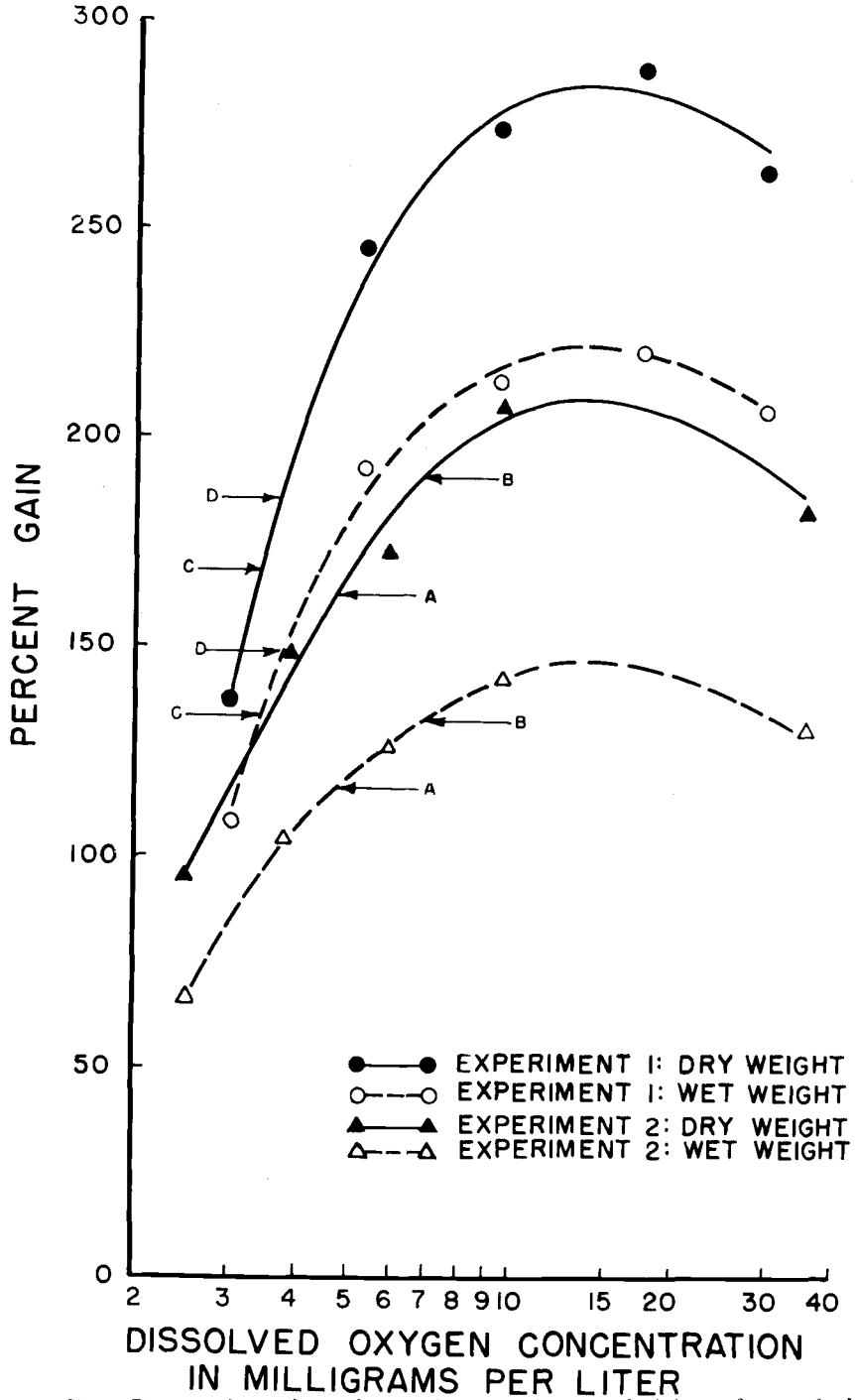

Figure 7. Percent gains in wet and dry weights, in relation to oxygen concentrations, in experiments 1 and 2. Arrows indicate weight gains in tests with fluctuating concentrations (A: 2.3–9.6 mg./l.; B: 4.9–35.5 mg./l.; C: 3.0–9.5 mg./l.; D: 3.0–18.0 mg./l.) and the constant concentrations at which the same weight gains presumably would have occurred.

Growth and Food Conversion with Restricted Diet

Table 2 shows that, in experiment 3, the gains in wet and dry weights, crude fat, fat-free dry matter, and calorific value of the fish kept on a uniform, restricted diet at various constant oxygen concentrations ranging from about 3 to 18.1 mg./l. did not differ greatly. The smallest weight gains (in grams and percent) were shown by the fish held at oxygen concentrations near 3 mg./l., the lowest mean concentration tested, and by those held at oxygen concentrations averaging 9.4 mg./l., near the air-saturation level. The largest gains were shown by the fish held at concentrations averaging 18.1 mg./l., nearly twice the air-saturation level. It is noteworthy that the percent gains in crude fat are all much greater than the corresponding percent gains in wet weight or in fat-free dry matter.

In Figure 8, the gains per fish in grams of dry weight, crude fat, and fat-free dry matter are plotted against oxygen concentration. No effect of oxygen concentration is indicated, except a possible impairment of growth at the lowest tested oxygen concentration (3 mg./l.). The indicated impairment of food conversion efficiency of the fish held at the lowest dissolved oxygen level is revealed also by the relatively low food conversion ratios for the fish shown in Table 3. Inasmuch as one fish died during experiment 3 in one of the two test vessels in which a mean oxygen concentration of 3 mg./l. was maintained, and it was necessary therefore to assume that the initial weight of the dead fish was equal to the mean initial weight of the entire group of fish held in the vessel, the

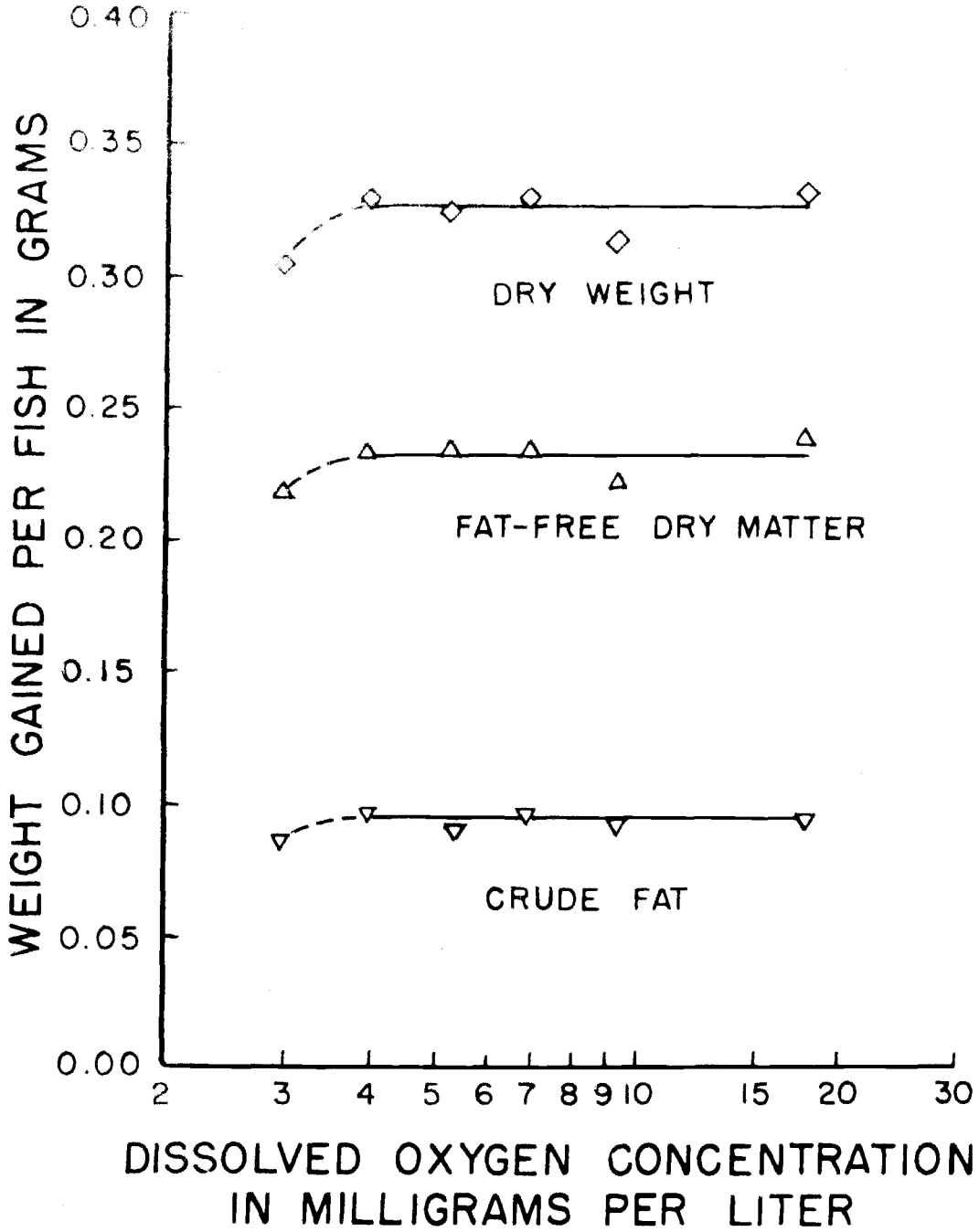

Figure 8. Weight gains per fish in grams, in relation to constant oxygen concentrations, experiment 3.

results in Tables 2 and 3 pertaining to that test vessel are not deemed entirely reliable. For this reason, results obtained at the lowest tested oxygen concentration only with those fish among which no deaths occurred have been included in Figure 7. However, the results reported in Table 2 for the other group of fish held at the same low oxygen concentration are not materially different, indicating only slightly smaller gains in dry weight, crude fat, and fat-free dry matter.

It should be noted that the two groups of fish that had been held at the lowest tested oxygen concentration of 3 mg./l. in experiment 3 were the groups that had the smallest mean initial weights (Table 1). Excepting these two groups, the group with the smallest mean initial weight was that which was held at oxygen concentrations near 18.1 mg./l. and showed the greatest gain in weight, and the group with the greatest mean initial weight was that which was held at oxygen concentrations near 9.4 mg./l. and showed the smallest gain in weight. The relatively poor growth of the fish held at 3 mg./l. dissolved oxygen evidently is not ascribable to the smaller initial size of the fish, which could be expected to favor growth of fish kept on a restricted diet, because the smaller fish had more food per gram of their initial weight.

DISCUSSION

In the experiments reported here, the growth rates of juvenile coho salmon at all oxygen concentrations tested were much greater than the growth rates observed by Herrmann, Warren, and Doudoroff (9, p. 161-162). Their fish showed mean wet weight gains in 21 days not exceeding 104 percent. It is believed that the test temperature of 18° C. probably is more favorable for the growth of salmon than 20° C., the temperature at which the experiments of Herrmann et al. were performed, but it is unlikely that the temperature difference alone explains the great difference in the growth rates observed at favorable oxygen concentrations. Tubificid worms may well be more easily digested and assimilated than the beach hoppers fed to fish by Herrmann et al., and also more nutritious. Finally, the source and history of the fish may have had an important influence also. It should be noted that in experiment 2 of this study, the growth of the coho salmon at any oxygen concentration was not as rapid as the growth in experiment 1 at the same oxygen concentration and temperature. The difference in observed growth rates in these two experiments may be attributable to the difference in source and history of the fish, or to the quality of the food (tubificids) collected from different sources for the two experiments. The tubificids used in experiment 1 were collected from the fish raceways of the Oregon State Game Commission's Roaring River trout hatchery, located in Linn County. For experiment 2, the tubificids

were collected from Oregon State University's experimental sewage treatment lagoons, located at Corvallis. The worms from the two sources have not yet been identified.

The difference in shape between the curves relating weight gains to oxygen concentrations which were obtained in this study and the more sharply inflected (somewhat angular) curve plotted by Herrmann et al. (9, p. 161) is not fully understood. The growth rates of the fish held at mean oxygen concentrations of 2.5 and 3.0 mg./l. in this study were markedly reduced, as compared with those of the controls, but the reduction was not as great, percentagewise, as that which was to be expected on the basis of the curve plotted by Herrmann et al. Possibly the same factors that were responsible for the difference in the growth rates of the fish at high oxygen concentrations were somehow responsible also for the difference in the shapes of the curves. Experimental or sampling errors also may have contributed to the latter difference, for the weight gains observed by Herrmann et al. in different tests were variable, especially at concentrations near 3 mg./l., where one of the two observed values may well have been unduly low for some reason.

A large fraction of the weight gain by each group of fish tested in this study was due to an increase in crude fat. The great increase in fatness of the fish even at low oxygen concentrations probably was due to consumption by the relatively inactive fish of a larger amount of an easily digested and nutritious food than is usually available under natural conditions. The ability of the salmon to

digest and assimilate such large amounts of food and to grow fatter at the low oxygen concentrations may be even more significant than the observed depression of growth rates. It must be realized, however, that such rapid growth might not have been possible, even in the presence of an abundance of nutritious food, under conditions necessitating more activity on the part of the fish.

The results of experiments 1 and 2 pertaining to the effects of fluctuating dissolved oxygen concentrations differ materially. It is not clear why fluctuations of oxygen concentration between a very low level and the air-saturation level had a much less depressing effect on growth in experiment 2 than in experiment 1. The observation that the depression of the growth rate of fish exposed alternately to moderately low and exceedingly high oxygen concentrations (4.9 and 35.5 mg./l.) in experiment 2 was not great is not so surprising, inasmuch as neither of these concentrations was found to have a markedly adverse effect on growth in tests of constant concentration. This result shows only that wide fluctuations of oxygen concentration per se do not greatly impair growth in the absence of decidedly adverse concentrations. Stewart (10, p. 24) also observed varying effects of fluctuating oxygen concentrations on the growth of largemouth bass, but concluded (10, p. 37) that "even when oxygen concentrations are near air-saturation levels during a large portion of each day, the growth of fish may be seriously inhibited if very low concentrations occur during the remainder of the 24-hour day." Stewart also

concluded (10, p. 37) that "the occurrence of oxygen concentrations (far above air-saturation) during daytime and thereafter, alternating with low concentrations occurring at night and early in the morning may be most detrimental, even though the daily mean oxygen concentrations are at levels which would be quite satisfactory if these concentrations persisted throughout the day with little variation." The results of the present study with coho salmon generally confirm these conclusions, even though the growth of salmon exposed alternately to 2.3 and 9.6 mg./l. in experiment 2 was better than the growth expected on the basis of earlier results. It is noteworthy that very high dissolved oxygen concentrations, up to nearly four times the air-saturation level, generally did not have as adverse an effect on the growth of coho salmon as on the growth of largemouth bass. This is somewhat surprising, in view of the fact that salmon are less apt than the bass to be exposed to such high oxygen concentrations in their natural habitats. Davis (4, p. 18-19) observed no adverse effect on the maximum sustained swimming speed of coho salmon of high oxygen concentrations up to about twice the air-saturation levels, but much higher concentrations were not tested by him.

In discussing dissolved oxygen criteria or standards for use in the regulation of waste disposal for the protection of fresh water fishes, Doudoroff (7, p. 249) has pointed out that, while criteria based on the assumption that low oxygen concentrations will persist only for short periods can be misleading, wide

diurnal and other variations of dissolved oxygen in many natural and polluted waters perhaps should not be entirely disregarded in establishing standards. Accordingly, the Aquatic Life Advisory Committee of the Ohio River Valley Water Sanitation Commission (2, p. 327) has recommended that permissible oxygen concentrations in waters in which well-rounded warm-water fish populations are to be sustained should be not less than 5 mg./l. during at least 16 hours of any 24-hour period, and not less than 3 mg./l. at any time. Although it has not been demonstrated in nature, impairment of the growth of fish that has been observed in this study and the study of Stewart (10, p. 1-44) when the fish were exposed daily to very low concentrations for only a portion (less than half) of each day raises some question as to the value and adequacy of such complex restrictions or standards as the above.

The unimpaired food conversion efficiencies of fish kept on an unrestricted diet at moderately reduced oxygen concentrations (3.8 mg./l. and above), in experiment 2 (Table 3), indicate that the observed depression of growth rates is due to the depressing influence of low oxygen concentration on the appetite. A lower food conversion ratio probably occurred at the 2.5 mg./l. dissolved oxygen level. These results agree with those of Herrmann et al. (9, p. 166), who pointed out that "some reduction of the food conversion ratios (gross conversion efficiencies) can be expected to result from the observed reduction of food consumption rates

at low oxygen concentrations, since the fraction of consumed food needed for satisfying constant maintenance requirements increases with a decrease of the rate of food consumption." They further suggested that, since conversion ratios remained high at 4 and 5 mg./l. dissolved oxygen, the maintenance food requirements may have been somewhat reduced through restriction of spontaneous activity, or the efficiency of food digestion and assimilation may have been increased, through reduction of the rate of food consumption. In view of the results of experiment 3 of the present study, in which coho salmon were kept on a rather severely restricted diet and showed almost uniformly high gross conversion efficiencies at all tested oxygen concentrations down to 4 mg./l., it appears that this suggestion can be dismissed. It seems probable that the maintenance food requirement is such a small fraction of the amount of food consumed by well-fed fish at moderately reduced oxygen concentrations, that it does not have a very important influence on the gross conversion efficiency. The maintenance food requirement may indeed vary with ambient oxygen concentration. However, the effect on the maintenance requirement of the reduction of over-all activity observed at low oxygen concentrations may be balanced, if not outweighed, by the opposite effect of the increased cost of respiration (i.e., opercular movements). In any event, the net effect of these variations in muscular activity on food conversion efficiency may be measurable only when the daily food ration is not much in excess of the maintenance

requirement.

A slight reduction of the food conversion ratio at the lowest oxygen concentration tested (3 mg./l.) was observed in the present study when fish were fed restricted rations (experiment 3). This observation suggests impairment of digestive or assimilatory efficiency at the low oxygen concentration, which already had been suggested by some data of Herrmann et al. (9, p. 163). It also supports the assumption that in experiment 2 only 14 fish were present in the test vessel throughout the test at 2.5 mg./l. dissolved oxygen. The food conversion ratio computed on the basis of a different assumption would appear to be too high.

The fact that higher food conversion ratios were observed when coho salmon were kept on a restricted diet than when they were kept on an unrestricted diet at high or low oxygen concentrations indicates that a considerable amount of food was wasted, through incomplete assimilation, by fish fed to repletion at any dissolved oxygen level. Brown (3, p. 387) noted that, when the food supply of brown trout, Salmo trutta, is restricted, the net conversion efficiency becomes greater as the daily food ration approaches the maintenance level. With more food than the maintenance requirement, but less than an unlimited amount, very high values for net efficiency may be observed, and the growth of the fish may be almost as rapid as that of fish kept on unrestricted rations under the same conditions. It should be noted again that no impairment of gross conversion efficiency was observed at oxygen concentrations

near 4 mg./l. in experiment 3 of this study, in which rations were restricted; yet the efficiency at these moderately reduced concentrations in experiment 2 (with unrestricted rations), was not greater than it was at high concentrations, although food consumption was materially reduced. It can be concluded that a reduction of food consumption probably can have a favorable effect on the food conversion efficiency only when it is not a reduction that is necessitated by adverse dissolved oxygen conditions.

BIBLIOGRAPHY

1. American Public Health Association, American Water Works Association, and Water Pollution Control Federation. Standard methods for the examination of water and wastewater, including bottom sediments and sludges. 11th ed. New York, American Public Health Association, Inc., 1960. 626 p.

2. Aquatic Life Advisory Committee of the Ohio River Valley Water Sanitation Commission. First progress report - aquatic life water quality criteria. Sewage and Industrial Wastes 27:321-331. 1955.

3. Brown, Margaret E. Experimental studies on growth. In: The Physiology of Fishes. Ed. by M. E. Brown. Vol. 1. Metabolism. New York, Academic Press, 1957. p. 361-400.

4. Davis, Gerald Evert. The influence of dissolved oxygen concentration on the swimming performance of juvenile coho salmon at different temperatures. Master's thesis. Corvallis, Oregon State University, 1960. 58 numb. leaves.

5. Davison, Robert C. et al. Experiments on the dissolved oxygen requirements of cold-water fishes. Sewage and Industrial Wastes 31:950-966. 1959.

6. Doudoroff, Peter. Water quality requirements of fishes and effects of toxic substances. In: The Physiology of Fishes. Ed. by Margaret E. Brown. Vol. 2. Behavior. New York, Academic Press, 1957. p. 403-430.

7. Doudoroff, Peter. How should we determine dissolved oxygen criteria for fresh water fishes? In: Biological Problems in Water Pollution: Transactions of the 1959 seminar, Robert A. Taft Sanitary Engineering Center. Cincinnati, Ohio, 1960. p. 248-250. (U.S. Public Health Service. Robert A. Taft Sanitary Engineering Center. Technical Report W60-3).

8. Haempel, O. Über die Wirkung höherer Sauerstoffkonzentration auf Fische nebst Untersuchungen über die Ausnützung des künstlich ins Wasser eingeleiteten O_2. Zeitschrift fur vergleichende Physiologie 7:553-570. 1928.

9. Herrmann, Robert B., Charles E. Warren and Peter Doudoroff. Influence of oxygen concentration on the growth of juvenile coho salmon. Transactions of the American Fisheries Society 91:155-167. 1962.

10. Stewart, Nelson E. The influence of oxygen concentration on the growth of juvenile largemouth bass. Master's thesis. Corvallis, Oregon State University, 1962. 44 numb. leaves.

11. Tarzwell, Clarence M. Water quality criteria for aquatic life. In: Biological Problems in Water Pollution: Transactions of the 1956 seminar, Robert A. Taft Sanitary Engineering Center. Cincinnati, Ohio, 1957. p. 246-272. (U.S. Public Health Service. Robert A. Taft Sanitary Engineering Center.)

12. Tarzwell, Clarence M. and Arden R. Gaufin. Some important biological effects of pollution often disregarded in stream surveys. In: Proceedings of the Eighth Industrial Waste Conference. Lafayette, Ind. 1953. p. 295-316. (Purdue University. Engineering Experiment Station. Bulletin. Series no. 83).

13. Townsend, L. D. and D. Earnest. The effects of low oxygen and other extreme conditions on salmonid fishes. In: Proceedings of the Sixth Pacific Science Congress of the Pacific Science Association. Berkeley, Calif., 1939. vol. 3. Berkeley, University of California Press, 1940. p. 345-351.

14. Wiebe, A. H. Diurnal variations in the amount of dissolved oxygen, alkalinity, and free ammonia in certain fish ponds at Fairport, (Iowa). The Ohio Journal of Science 31:120-126. 1931.

15. Wiebe, A. H. and Alfred M. McGavock. The ability of several species of fish to survive on prolonged exposure to abnormally high concentrations of dissolved oxygen. Transactions of the American Fisheries Society 62:267-274. 1932.

16. Woodbury, Lowell A. A sudden mortality of fishes accompanying a supersaturation of oxygen in Lake Waubesa, Wisconsin. Transactions of the American Fisheries Society 71:112-117. 1941.