

THE INFLUENCE OF OXYGEN
CONCENTRATION ON THE GROWTH OF
JUVENILE LARGEMOUTH BASS

by

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INTRODUCTION

A laboratory study was undertaken in order to determine the influence of dissolved oxygen concentration on the growth of juvenile largemouth bass, Micropterus salmoides (Lacépède). Six experiments were performed during the period from April to November, 1961, at the Oak Creek Laboratory of the Pacific Cooperative Water Pollution and Fisheries Research Laboratories, Oregon State University. The influence of nearly constant oxygen concentrations both below and above the air-saturation level, and also of wide diurnal fluctuations of oxygen concentration upon the growth, food consumption, and food conversion efficiency of juvenile largemouth bass at temperatures near 26° C. was determined. The fish were kept on an unrestricted diet of earthworms.

Fresh-water fishes may be exposed to various concentrations of dissolved oxygen in their natural environment. In some waters, especially those receiving putrescible organic wastes such as municipal sewage, the dissolved oxygen concentration may be reduced to low levels for long periods of time, or large diurnal fluctuations of oxygen concentration may occur. Dissolved oxygen is reduced through oxidative decomposition of organic matter in the water by bacterial action, and products of this decomposition, such as carbon dioxide, nitrates and phosphates, can be utilized as nutrients

by algae and so can cause algal "blooms." In water rich in plant nutrients, the oxygen concentration may rise to very high levels during the day, because of the photosynthetic activity of algae and other aquatic plants, whereby oxygen may be produced much more rapidly than it is being consumed. At night, the concentration may drop to very low levels because of respiratory consumption of oxygen by the algae and other aquatic organisms and bacterial action on remaining organic matter. Tarzwell and Gaufin (15, p. 300) reported that at one station in Lytle Creek, a small stream in southern Ohio polluted with municipal sewage, the dissolved oxygen varied from 19.4 milligrams per liter (mg./l.) in the afternoon to 0.7 mg./l. the next morning. Greater fluctuations in dissolved oxygen concentration are possible in large, slow streams and in standing waters. Oxygen concentrations as high as 27.6 mg./l. and 32.1 mg./l. have occurred in ponds and lakes (17, p. 126) (20, p. 115).

The influence of low concentrations of dissolved oxygen on the survival of fresh-water fishes has been frequently investigated. Doudoroff (8, p. 413-415) has briefly discussed the limits of tolerance of fresh-water fishes to low oxygen concentrations. Moss and Scott (12, p. 383-385) have reported that at 25° C. critical dissolved oxygen levels for largemouth bass weighing 4.7, 7.8, and 23.9 grams were 0.78, 0.87, and 0.84 mg./l., respectively. They determined these levels by placing the experimental fish in flowing air-saturated water and then gradually reducing the oxygen content of the water each day until the fish died.

A few investigations of the influence of subsaturation levels of dissolved oxygen on the growth and food utilization of salmonid fishes have been reported (13, p. 1231-1232) (6, p. 957) (11, p. 161-167). To the best of the author's knowledge, no such studies on warm-water fishes have been reported in the literature, nor any studies of the influence of dissolved oxygen concentrations well above the air-saturation level and of wide diurnal fluctuations of oxygen concentrations on the growth, food consumption, and food conversion efficiency of any fresh-water or marine fishes. Doudoroff (9, p. 249) has pointed out that experimental data bearing on the latter problem are much needed as factual basis for the establishment of dissolved oxygen criteria for fresh-water fishes.

Herrmann, Warren, and Doudoroff (11, p. 161-167) found that growth and food consumption rates of underyearling juvenile coho salmon, Onchorhynchus kisutch, which were held in fresh water at 20° C. and fed beach hoppers (marine amphipods) to repletion, declined slightly as the oxygen concentration was reduced from about 8.3 to 6 and 5 mg./l., and declined more sharply as the oxygen concentration was reduced further. At concentrations averaging 2.1 to 2.3 mg./l. many fish died and surviving fish consumed very little food and lost weight. Gross food conversion efficiencies were markedly reduced at oxygen concentrations below 4 mg./l. only. Earlier studies that have demonstrated a pronounced influence of nonlethal reduced oxygen concentration on the growth of yearling coho salmon (6, p. 957) and of sac fry of Salmo salar relictus (13, p. 1231-1232)

have been briefly summarized and discussed by Herrmann, Warren, and Doudoroff (11, p. 155-156).

Abnormally high concentrations of dissolved oxygen have been long ago reported harmful and fatal to fish by Haempel (10, p. 553-570). However, other investigators have reported that different fishes could tolerate very high oxygen concentrations for prolonged periods. Wiebe and McGavock (18, p. 267-274) found that various centrarchids, salmonids, and cyprinids were able to withstand long exposures to oxygen concentrations ranging from about two to more than three times the air-saturation values. Wiebe (19, p. 117) reported that fingerling largemouth bass tolerated concentrations as high as 40 mg./l., or 410 percent of the air-saturation level. Food consumption and growth rates of the fish were not determined by these investigators.

The experimental results presented in this thesis show adverse effects of both low and abnormally high nonlethal oxygen concentrations and of wide diurnal fluctuations of oxygen concentration on the growth of juvenile largemouth bass.

EXPERIMENTAL APPARATUS, MATERIALS AND METHODS

Experimental Apparatus

The experimental apparatus used in this study was designed to provide a constant flow of water of controlled temperature and dissolved oxygen content to bottles containing the test fish. The apparatus was located in a 25° C. constant-temperature room that was illuminated with fluorescent lights. The apparatus is pictured in Figures 1 and 2. Figure 2 is a schematic drawing and shows only one of seven units that comprised the experimental apparatus.

This apparatus was similar in design and function to that described by Davison et al. (6, p. 952-953) except for provision made for recirculation of the water. Therefore, only a general description of the pattern of water flow through the apparatus will be given in this thesis.

Filtered water supplied from a small spring-fed stream was introduced into an overflowing 5-gallon constant-head jar of Pyrex glass. From here 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 warmed water then flowed through a 1-gallon jar, containing the thermoregulator, into a glass column where it was vigorously aerated with air from an electric diaphragm-actuated air pump. This was done to bring the dissolved oxygen concentration to near the saturation level. Next, the water flowed through a 1-gallon distribution jar to seven vertical

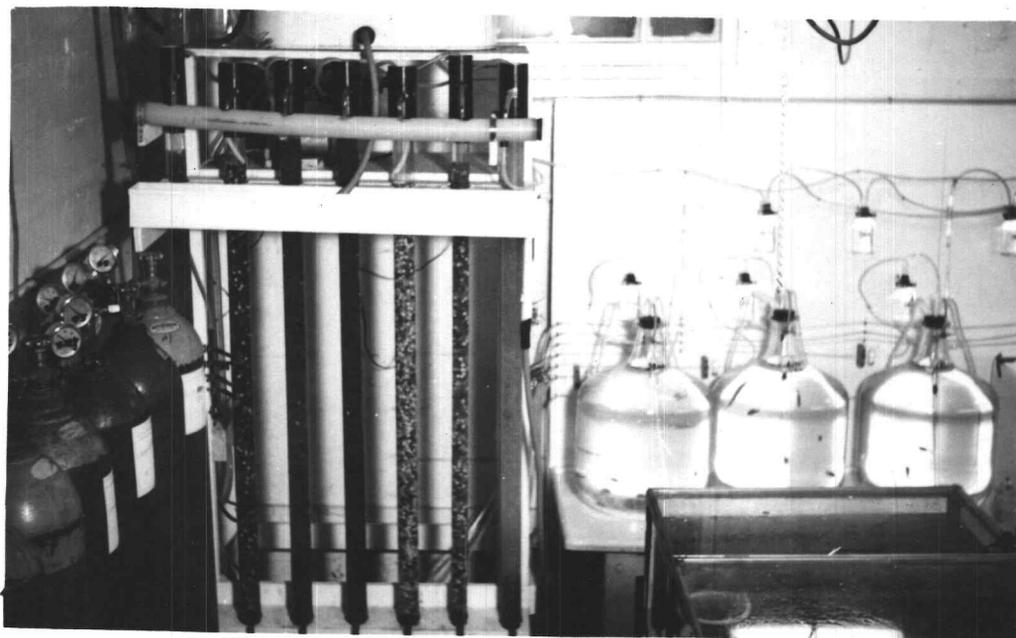
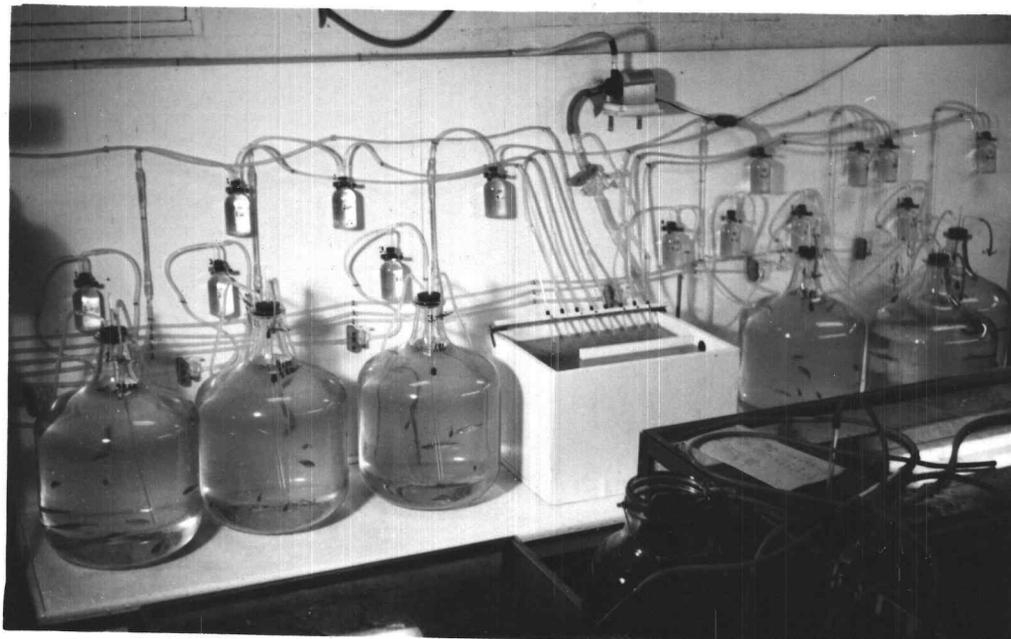


Figure 1. Two views of the experimental apparatus.

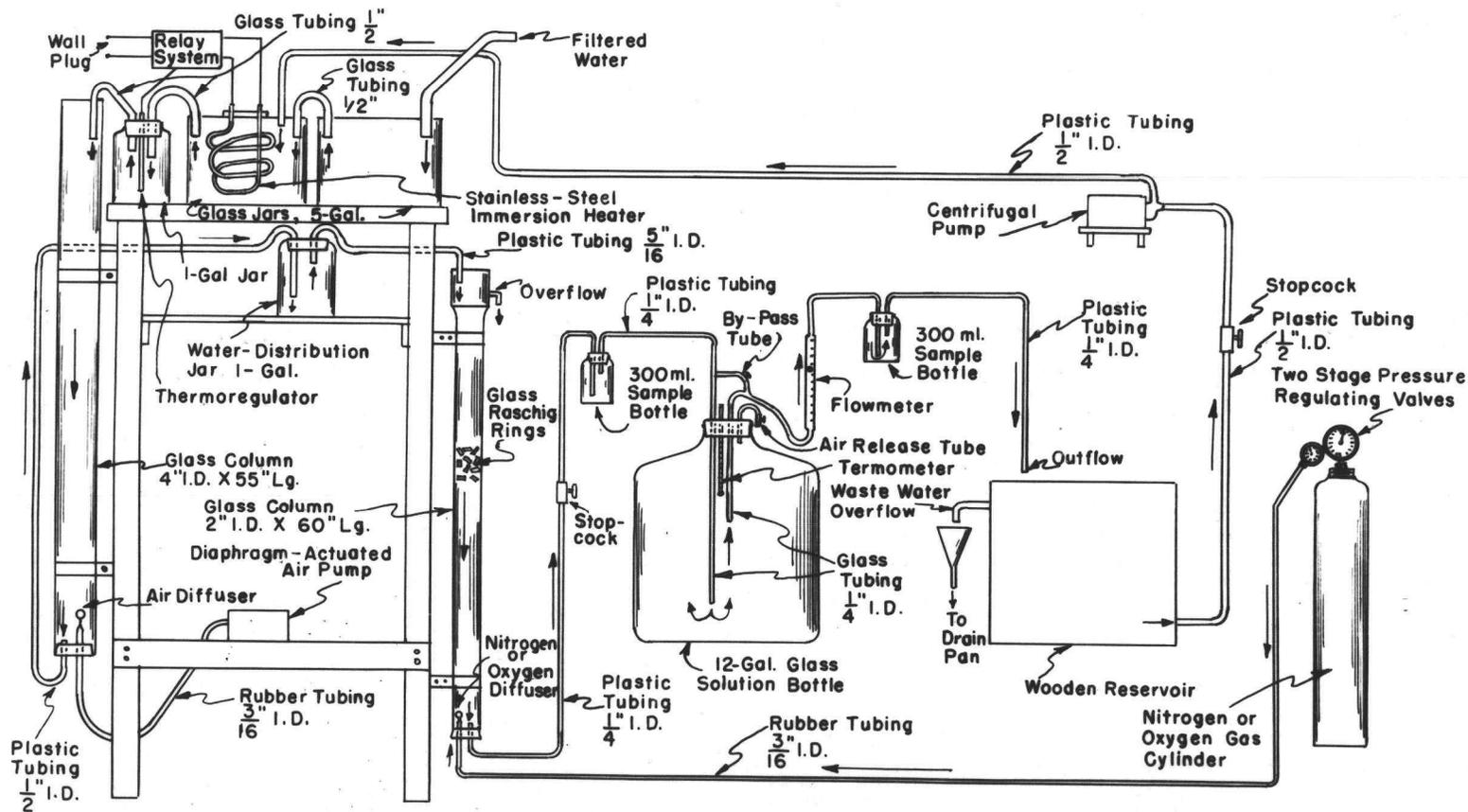


Figure 2. Schematic drawing of the experimental apparatus. One of seven units is shown.

glass columns packed with Raschig rings, where constant hydraulic heads were maintained by overflow. The desired level of dissolved oxygen in the water leaving each column was attained by introducing nitrogen or oxygen at an appropriate rate through a gas disperser at the base of the column.

After leaving the glass column at the bottom, the water was conducted by 1/4-inch flexible plastic tubing (Tygon, No. R-3603) through a flow-adjustment stopcock and a 300-milliliter sample bottle into a stoppered 12-gallon Pyrex glass solution bottle, which served as the test vessel. A by-pass tube connecting the inflow and outflow tubes of a test vessel made it possible to maintain a constant water flow through the rest of the system when the stopper of a test vessel was removed. The water flowing out of each test vessel passed through a ball-displacement flowmeter, through another 300-milliliter sample bottle, and into a wooden reservoir. Part of the discharged water (approximately 80 percent in the first two experiments and 70 percent in the remaining experiments) was then returned by a centrifugal pump to the Pyrex glass jar containing the immersion heater. This was necessary for conserving the heated water. Flows near 500 milliliters per minute were maintained through each test vessel. Water temperatures in the test vessels were measured by thermometers inserted through the rubber stoppers.

Experimental Material

The juvenile largemouth bass used in these experiments were seined from various ponds in the Willamette River Valley of Oregon.

It was necessary to use fish from different sources because the required number of fish of the desired size could not always be obtained from the same source. However, fish from one source only were used in any single experiment.

The fish used in experiment 1 were secured from Falk's Bass Farm north of Harrisburg and were held for five months in a pond at the laboratory before use. Fish for experiment 2 were obtained from a gravel pit about five miles north of Albany. These fish were held about one month in a trough before use. The fish used in experiments 3 and 4 were taken from Oregon State University's Soap Creek experimental ponds north of Corvallis about one week before the experiments were begun. Fish used in experiment 5 were obtained about one week before the experiment started from a farm pond belonging to W. P. Grossen near Cornelius. Fish for experiment 6 were seined from gravel-pit ponds near Corvallis and were held for three months in a pond at the laboratory before they were used. The fish used in experiments 1 and 2 were from the 1960 brood and had mean initial lengths of 61.8 millimeters and 84.5 millimeters, respectively. The fish used in the remaining experiments were from the 1961 brood, and the mean initial lengths ranged from 64.3 millimeters to 73.2 millimeters.

Experimental Methods

The test fish were acclimated to the experimental temperature of 26° C. for a period of three to ten days in a 50-gallon aquarium

before being used in an experiment. During this time the fish were fed a mixed diet of earthworms, cladocera, and mosquito larvae until 24 hours before their transfer to the test vessels. Several fish of each lot were examined for parasites and disease before the experiment. The fish used in experiment 5 had a mild bacterial infection, which was successfully treated with Aureomycin before the fish were placed in the test vessels. The fish were treated for approximately two days at a dosage of 14 grains of Aureomycin per gallon of water, as recommended by the manufacturer.

The experimental apparatus was put into operation at least 24 hours before the beginning of an experiment, so as to replace all the water in the system with fresh water having the desired temperature. Oxygen concentrations were kept at the air-saturation level until after the fish had been placed into the test vessels.

The fish used in an experiment were as nearly as possible uniform in size. They were lightly anesthetized with MS 222 (Tricane methanesulphonate), weighed and measured, and then placed into the test vessels. The fish were weighed out of water after removing excess moisture by blotting with paper towels. Ten fish were placed into each test vessel. A sample of 10 fish taken at the beginning of each experiment was used to determine the ratio of dry weight to wet weight. This ratio was used in computing the initial dry weight of all the fish used in that experiment.

After the fish had been placed in the test vessels, the dissolved oxygen concentrations were adjusted to the desired levels

over a period of about 8-hours. 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., except during experiment 1, when the lights came on at 6:00 a.m. and went off at 12:00 p.m. Experimental feeding of the fish was begun in the morning of the following day.

The experimental conditions were maintained by making the necessary measurements and adjustments twice daily throughout the tests. The first check was made between 7:00 and 9:00 a.m. and the second check was made approximately eight hours later. During these checks, flowmeter readings and water temperatures were recorded. Water samples for dissolved oxygen determinations were obtained by removing the 300-milliliter sample bottles through which the inflowing and outflowing water passed and replacing them with other sample bottles. No adjustments of the apparatus were made until after the water samples had been taken. All dissolved oxygen determinations were made by the Alsterberg (azide) modification of the Winkler method (1, p. 309-312).

In experiments in which the influence of fluctuating dissolved oxygen concentrations was being studied, the fish in two or three of the test vessels were subjected to a low level and then a higher level of dissolved oxygen for definite portions of each day. In some experiments oxygen levels were changed every 12 hours, the oxygen content of the water flowing into the test vessels being reduced at 10:00 p.m. and increased at 10:00 a.m. In other experiments the oxygen levels were changed at intervals of 8 and 16 hours,

the low level being maintained for either 8 or 16 hours of each day and the high level for the remainder of the day. In these experiments, the oxygen content of inflowing water was reduced at either 4:00 p.m. or 12:00 p.m. and was increased always at 8:00 a.m.

In all experiments, the fish in each test vessel were fed daily small live earthworms. At least two different species of worms were represented and they have not yet been identified. In the first experiment, the fish were fed twice a day; the first feeding was between 8:00 and 10:00 a.m., and the second feeding was at least six hours later. In all of the other experiments, the fish were fed once a day between 8:00 and 10:00 a.m. In all experiments, an attempt was made to supply enough earthworms at each feeding to ensure a surplus remaining in each test vessel at the time of the next feeding. The supply of food provided was exhausted by the time of the next feeding on a few occasions only, mostly in experiment 1. Uneaten earthworms and excrement were siphoned from the test vessels each time the fish were fed. All earthworms were weighed before being placed in the test vessels and all uneaten earthworms were weighed after removal from the test vessels, in order to determine the quantity consumed. The earthworms were weighed out of water after excess moisture had been removed by blotting with paper towels.

In all of the experiments except the first experiment, the earthworms were held for approximately 20 hours in water at 26° C. before they were fed to the fish. This was done to minimize changes

in weight of the worms, due to loss of silt from the intestinal tract or to osmotic uptake of water. However, the wet weight of worms from four of five samples taken at different times decreased by 3 to 15 percent after the worms had been held in water for 24 additional hours. The average loss in weight of these four samples was 7.5 percent. The first two samples of worms examined in July showed very little change in weight, the change varying only from 1 percent gain to 3 percent loss. For this reason, the need for determination of changes in wet weight of the worms was not immediately realized, but subsequent tests showed that these changes could be considerable at other seasons of the year, and should have been determined for each experiment. The amount of uneaten earthworms removed from the test vessels ranged from 7 to 40 percent of the amount fed, the average being 21 percent. Percentagewise, more food was left uneaten in test vessels having low oxygen concentrations than in test vessels having high oxygen concentrations (e.g., 30 percent on the average at 1.6 to 2.8 mg./l. dissolved oxygen, and 15 percent at 8.0 to 10.1 mg./l. dissolved oxygen). The wet weights of uneaten earthworms have not been corrected for the above mentioned changes, because adequate data for each experiment was lacking and the weight changes of the five different samples of worms were highly variable. Thus, the values given in this thesis for total wet weights of food consumed by groups of fish are usually somewhat higher than the true values. The maximal error, computed on the basis of the data from the five different samples of worms,

was found to be near 11 percent, but the average error is believed to be only about 2 percent.

The "percent dry weight" of earthworms (i.e., dry weight expressed as a percentage of the wet weight) also changed while the worms were held in water. The percent dry weight of worms that had been held in water for 20 hours only was higher than the percent dry weight of worms that had been held in water for 24 additional hours. The initial percent dry weight of earthworms fed to the fish at different times also varied. The percent dry weight of the worms that had been held in water for 20 hours increased from about 16 percent in June to about 20 percent in late October. The worms used in October appeared to have more residual silt in the intestinal tract than did worms used earlier. The seasonal change in percent dry weight of the worms was not clearly evident until experiment 6 was begun in October. Therefore, the percent dry weight of worms fed to the fish was not determined for each experiment. A mean percent dry weight has been computed from data obtained using six different samples of worms taken at different times during the course of the experiments. Dry weight percentages for earthworms that had been held in water for 20 hours and also for 44 hours were determined for each sample. The values obtained with the six samples were averaged to obtain a mean percent dry weight of 17 percent. This value was used to compute the dry weight of food consumed in each test vessel in all experiments.

At the conclusion of an experiment the oxygen concentrations were returned to near the saturation level in all test vessels. The fish were then held for about 24 hours without food before final weights were determined. After final wet weights had been obtained, all of the fish were dried at 70° C. for at least five days and their dry weights were determined.

RESULTS

The results of six experiments conducted from April to November, 1961, are summarized in Tables 1 and 2. All of the experiments except the first one were designed for determining the effects of diurnal fluctuations of dissolved oxygen concentration on the food consumption and growth of juvenile largemouth bass, as well as the effects of different constant concentrations. Tests at concentrations well above the saturation level were included in four of the experiments.

Table 1 shows the inclusive dates and duration of each experiment, the oxygen concentrations (means and ranges) recorded for the several test vessels in each experiment, the mean initial wet and dry weights of the fish tested at each oxygen concentration, and the changes in mean wet and dry weights of the fish. The mean initial weight of the fish is the mean weight of those fish that survived. In most cases, the initial weights of those fish that died could be reliably established and these initial weights were subtracted from the total initial weights of the fish in the test vessels in computing the mean initial weights of surviving fish. When the initial weight of a dead fish could not be established, it was assumed to have been equal to the mean initial weight of the ten fish used in the test. In all experiments, there was a total loss of only seven fish of which no more than one fish died at any one oxygen concentration tested in an experiment. The initial and final dates of each experiment shown in Table 1 are

TABLE 1

Growth of Surviving Juvenile Largemouth Bass at Various Dissolved Oxygen Concentrations

Experiment Number and Test Period	Test Vessel Number	Dissolved Oxygen (mg./l.)		Mean Initial Weight Fish (grams)		Wet Weight Gain per Fish		Dry Weight Gain per Fish	
		Mean	Range ^{1/}	Wet	Dry ^{2/}	Grams	Percent	Grams	Percent
Experiment 1. 4/10-4/25/61 (15 days)	5	1.6	1.4-2.1	2.47	0.55	0.37	15	0.11	20
	2	2.3	1.9-3.8	2.58	0.57	1.54	60	0.38	67
	4	3.0	2.7-3.8	2.65	0.59	2.50	94	0.64	108
	3	4.2	3.9-5.1	2.48	0.55	3.35	135	0.84	153
	1	5.8	5.5-6.4	2.71	0.60	3.75	138	0.94	157
	6	8.1	7.6-9.0	2.46	0.55	3.74	152	0.95	173
Experiment 2. 6/22-7/7/61 (15 days)	5 ^{3/}	1.7	1.5-2.0	6.55	1.55	-0.49	-7	-0.10	-6
	2	2.6	2.3-3.2	6.13	1.45	1.80	29	0.45	31
	4	3.7	3.5-4.4	6.90	1.63	3.37	49	0.87	53
	3	5.4	4.9-5.9	6.90	1.63	4.57	66	1.18	72
	6	8.2	7.3-9.9	7.06	1.67	6.24	88	1.59	95
	1	1.8-3.7 ^{4/}	1.7-4.6	6.33	1.50	1.74	27	0.47	31
	7 ^{3/}	1.9-8.3 ^{4/}	1.6-10.5	6.85	1.62	3.02	44	0.80	49
Experiment 3. 7/28-8/7/61 (11 days)	2	2.0	1.8-2.3	3.44	0.76	1.76	51	0.35	46
	4 ^{3/}	3.4	3.2-3.5	3.50	0.77	2.89	83	0.64	83
	3	5.9	5.6-7.0	3.13	0.69	3.92	125	0.86	125
	5 ^{3/}	10.0	9.6-10.9	3.21	0.70	3.48	108	0.86	123
	6	17.5	17.0-18.4	3.25	0.71	3.34	103	0.81	114
	1	2.1-5.9 ^{4/}	1.9-6.9	3.39	0.74	2.47	73	0.51	69
	7	2.1-17.4 ^{4/}	1.9-18.0	3.40	0.75	2.47	73	0.53	71
Experiment 4. 8/20-9/4/61 (15.5 days)	6	2.1	1.9-3.4	3.36	0.76	1.83	54	0.43	57
	3	3.4	3.0-3.8	3.42	0.77	3.59	105	0.81	105
	4	5.9	5.6-6.9	3.52	0.80	4.29	122	1.02	128
	5	10.1	9.5-10.9	3.36	0.76	4.18	124	1.00	132
	2	17.5	8.8-18.4	3.36	0.76	4.00	119	0.97	128
	1	2.1-5.9 ^{4/}	1.8-6.6	3.32	0.75	2.72	82	0.63	84
	7	2.0-17.4 ^{4/}	1.8-18.4	3.48	0.79	2.46	71	0.57	72
Experiment 5. 9/23-10/8/61 (15 days)	5 ^{3/}	1.9	1.8-2.8	4.16	0.93	2.10	50	0.56	60
	2 ^{3/}	3.2	2.8-3.8	4.38	0.98	3.98	91	1.02	104
	7	5.1	4.6-6.2	4.07	0.91	4.94	121	1.28	141
	1	8.0	6.8-8.9	4.29	0.96	6.50	152	1.68	175
	6 ^{3/}	24.1	23.3-27.0	4.11	0.92	4.17	101	1.12	122
	3	1.9-8.3 ^{5/}	1.8-10.7	4.11	0.92	2.96	72	0.76	83
	4	2.0-8.0 ^{6/}	1.8-9.9	4.42	0.99	3.78	86	0.98	99
Experiment 6. 10/19-11/3/61 (15 days)	3	1.9	1.6-2.8	3.39	0.84	1.26	37	0.30	36
	4	3.8	3.5-4.6	3.25	0.80	2.88	89	0.68	85
	6	8.1	7.4-9.2	3.19	0.79	2.79	87	0.65	82
	1	23.8	23.2-24.5	3.32	0.82	3.58	108	0.89	109
	7	3.8-24.1 ^{4/}	3.4-25.6	3.28	0.81	2.38	73	0.55	68
	2	1.8-8.5 ^{2/}	1.4-10.0	3.26	0.81	1.63	50	0.37	46
5	1.8-8.1 ^{6/}	1.4-10.0	3.43	0.85	2.61	76	0.62	73	

^{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 10 fish taken at the beginning of each experiment.

^{3/} One fish of the initial group of 10 fish died in the vessel during the experiment.

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

^{5/} The fish were subjected each day to oxygen concentrations near the lower level shown (mean low concentration) about twice as long as they were subjected to concentrations near the upper level shown (mean high concentration).

^{6/} The fish were subjected each day to oxygen concentrations near the lower level shown (mean low concentration) about half as long as they were subjected to concentrations near the upper level shown (mean high concentration).

TABLE 2

Food Consumption and Conversion by Largemouth Bass at Various Dissolved Oxygen Concentrations

Experiment Number and Test Period	Mean Oxygen Concentration (mg./l.)	Grams of Food Consumed per Fish ^{4/}		Grams of Food Consumed per Day per Gram Initial Weight of Fish ^{1/,2/}		Food Conversion Ratio ^{2/,3/}	
		Wet Weight	Dry Weight	Wet Weight	Dry Weight	Wet Weight	Dry Weight
Experiment 1. 4/10-4/25/61 (15 days)	1.6	4.77	0.81	0.129	0.098	0.078	0.136
	2.3	9.46	1.61	0.244	0.188	0.163	0.236
	3.0	14.04	2.39	0.353	0.270	0.178	0.268
	4.2	17.42	2.96	0.468	0.359	0.192	0.284
	5.8	19.54	3.32	0.481	0.369	0.192	0.283
	8.1	19.02	3.23	0.515	0.391	0.197	0.294
Experiment 2. 6/22-7/7/61 (15 days)	1.7	7.54	1.28	0.077	0.055		
	2.6	16.03	2.73	0.174	0.126	0.112	0.165
	3.7	23.09	3.93	0.223	0.161	0.146	0.221
	5.4	29.47	5.01	0.285	0.205	0.155	0.236
	8.2	34.93	5.94	0.330	0.237	0.179	0.268
	1.8-3.7 ^{4/} 1.9-8.3 ^{4/}	15.81 20.83	2.69 3.54	0.167 0.203	0.120 0.146	0.110 0.145	0.175 0.226
Experiment 3. 7/28-8/8/61 (11 days)	2.0	8.47	1.44	0.224	0.172	0.207	0.243
	3.4	12.07	2.05	0.313	0.242	0.239	0.312
	5.9	16.27	2.77	0.473	0.365	0.241	0.310
	10.0	15.55	2.64	0.440	0.343	0.224	0.326
	17.5	15.35	2.61	0.429	0.334	0.218	0.310
	2.1-5.9 ^{4/} 2.1-17.4 ^{4/}	11.11 10.97	1.89 1.86	0.298 0.293	0.232 0.225	0.222 0.225	0.270 0.285
Experiment 4. 8/20-9/4/61 (15.5 days)	2.1	10.90	1.85	0.209	0.157	0.168	0.232
	3.4	17.87	3.04	0.337	0.255	0.201	0.266
	5.9	20.76	3.53	0.380	0.285	0.207	0.289
	10.1	21.08	3.58	0.405	0.304	0.198	0.279
	17.5	19.83	3.37	0.381	0.286	0.202	0.288
	2.1-5.9 ^{4/} 2.0-17.4 ^{4/}	14.43 13.98	2.45 2.38	0.280 0.259	0.211 0.194	0.188 0.176	0.257 0.239
Experiment 5. 9/23-10/8/61 (15 days)	1.9	15.26	2.59	0.245	0.186	0.138	0.216
	3.2	25.88	4.40	0.394	0.299	0.154	0.232
	5.1	28.73	4.88	0.471	0.358	0.172	0.262
	8.0	36.65	6.23	0.570	0.433	0.177	0.270
	24.1	25.33	4.31	0.411	0.312	0.165	0.260
	1.9-8.3 ^{5/} 2.0-8.0 ^{6/}	19.50 24.12	3.32 4.10	0.316 0.364	0.241 0.276	0.152 0.157	0.229 0.239
Experiment 6. 10/19-11/3/61 (15 days)	1.9	10.23	1.74	0.201	0.138	0.123	0.172
	3.8	16.97	2.88	0.348	0.240	0.170	0.236
	8.1	18.24	3.10	0.381	0.262	0.153	0.210
	23.8	20.93	3.56	0.420	0.289	0.171	0.250
	3.8-24.1 ^{4/}	14.69	2.50	0.299	0.206	0.162	0.220
	1.8-8.5 ^{5/} 1.8-8.1 ^{6/}	11.03 15.58	1.88 2.65	0.226 0.303	0.155 0.208	0.148 0.168	0.197 0.234

^{1/} Computed mean for those fish that survived to the end of the test.

^{2/} Values in the wet weight column and the dry weight column are based on wet weights of both fish and food and on dry weights of both fish and food, respectively.

^{3/} Weight gain per fish in grams (see Table 1) divided by the total weight of food consumed per fish in grams.

^{4/,5/,6/} See correspondingly numbered footnotes in Table 1.

the date of the first feeding and the date on which the uneaten food from the last feeding was removed from the test vessel.

Table 2 shows the total wet and dry weights in grams of food consumed per surviving fish during each test. In computing these values for a test in which a fish died, it was assumed that the fish that died consumed as much food per day up to the day of its death as did those fish that survived to the end of the test. The values computed on this basis may be slightly low, because the fish that were about to die probably did not feed as well as the surviving fish. However, the error would be small, because no more than one fish (10 percent) died during a single test.

Table 2 also shows for each test the average weight in grams of food consumed per day per gram of initial weight of the fish. Values based on both wet and dry weights are given (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). They were computed by dividing the number of grams of food consumed per day per surviving fish by the mean initial weight of these fish in grams. Table 2 further shows the mean food conversion ratios based on both wet and dry weights for surviving fish in each test in which the fish gained weight. A food conversion ratio was computed by dividing the mean gain in weight of the fish in grams by the number of grams of food consumed per fish during the test, using wet weights only or dry weights only.

Growth

The data in Table 1 show that, when juvenile largemouth bass were held at temperatures near 26° C. and fed small live earthworms, their growth was markedly influenced by dissolved oxygen concentration. Figure 3 shows the percent gain in dry weight plotted against oxygen concentration for each group of fish tested at a constant oxygen concentration. A curve has been fitted by eye to the points representing the results of each separate experiment. The percent gains in dry weight, rather than gains in wet weight, have been plotted because they are believed better to represent the relative amounts of consumed food substance that had been incorporated in the bodies of the fish. A difference in relative water content of the fish has been observed. The fish held at oxygen concentrations near the air-saturation level usually had a higher percent dry weight than fish held at lower oxygen concentrations (Appendix Table A). This is believed to indicate a higher content of stored fats in the tissues of the fish from the higher oxygen concentrations.

Figure 3 shows that the percent gain in dry weight of the fish increased as the oxygen concentration increased up to the air-saturation level, which is about 8.2 mg./l. at 26° C. (1, p. 312). The growth of fish held at oxygen concentrations well above the air-saturation level was generally depressed, as compared with growth at concentrations near the air-saturation level. The mean percent weight gains of fish held for 15 days at nearly the same oxygen

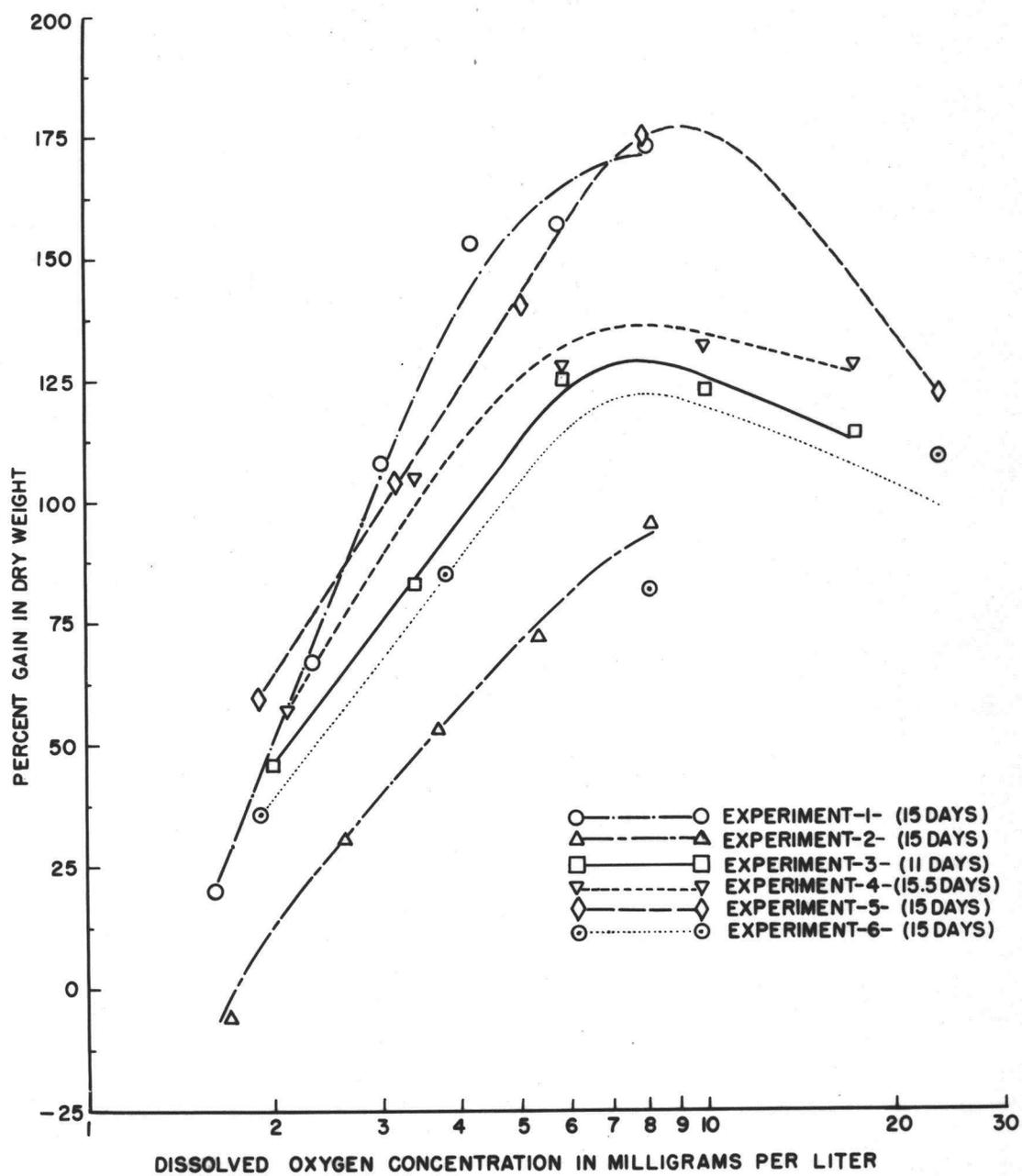


Figure 3. Gain in weight of largemouth bass, in relation to dissolved oxygen concentration.

concentrations in different experiments varied greatly. For example, in experiment 1, fish held at mean oxygen concentrations of 1.6 mg./l. and 8.1 mg./l. increased in dry weight by 20 and 173 percent, respectively, whereas in experiment 2, fish held at a mean oxygen concentration of 1.7 mg./l. decreased in dry weight by 6 percent, and fish held at a mean oxygen concentration of 8.2 mg./l. increased in dry weight by only 95 percent. It should be noted that the duration of experiment 3 (11 days) was much shorter than that of the other experiments, and that the relative position of the corresponding curve is affected thereby. The percent weight gains doubtless would have been much greater after 15 days.

The gain in weight of the fish held at a mean oxygen concentration of 8.1 mg./l. in experiment 6 was apparently much less than it should have been, judging by the somewhat greater weight gains observed at the next lower and higher tested concentrations. It can be seen that in all the other experiments the growth at concentrations near 8 mg./l. was decidedly faster than growth at concentrations well below and far above this value. The cause of the relatively slow growth of the fish held at 8.1 mg./l. dissolved oxygen in experiment 6 is unknown. Unusually violent or persistent aggression by one of the fish in the test vessel may possibly have occurred, and this may have interfered with feeding and impaired the growth of the other fish. The dotted curve in Figure 3 that pertains to experiment 6 was drawn so that it would nearly parallel, or would correspond in shape to the curve based on the

results of experiment 3. The latter curve seems to represent a typical or nearly average relationship between dissolved oxygen concentration and the growth of juvenile largemouth bass. It will be noted that this curve is intermediate in shape between those fitted to the points representing the results of experiments 4 and 5. When a similar curve was fitted to data from experiment 6, it was thought best to disregard the low observed percent gain in weight of the fish held at a mean oxygen concentration of 8.1 mg./l. in this experiment, and to assume that the value obtained at 24 mg./l. dissolved oxygen was somewhat too high. The shape of the hypothetical curve shown in Figure 3 for experiment 6 may be inappropriate; however, it is believed that a curve fitted to all of the data without reference to the results of the other experiments probably would have been more seriously erroneous than the curve that is shown.

Table 3 shows the percent gain in weight of fish held at diurnally fluctuating dissolved oxygen concentrations, the mean daily maximum and minimum oxygen concentrations for each of the tests, and the approximate mean oxygen concentrations (arithmetic and geometric means) to which the fish were exposed throughout the tests. The latter are arithmetic and geometric means of the mean upper and mean lower extremes, weighted according to exposure time when the periods of exposure to low and high concentrations were not equal. Table 3 also shows the approximate gain in dry weight of bass that presumably would have occurred had the fish been held

TABLE 3

Comparison of Dry Weight Gains of Bass 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 and Test Period	Approximate (mean) Limits of Dissolved Oxygen Fluctuations (mg./l.)		Approximate Mean Dissolved Oxygen Concentration (mg./l.) ^{1/}		Observed Gain in Dry Weight ^{2/} (Percent)	Estimated Gain in Dry Weight (Percent) ^{3/} at Constant Oxygen Concentration Equal to:	
	Mean Low D.O.	Mean High D.O.	Arithmetic Mean	Geometric Mean		Arithmetic Mean D.O.	Geometric Mean D.O.
	Experiment 2. 6/22-7/8/61 (15 days)	1.8 1.9	3.7 ^{4/} 8.3 ^{4/}	2.8 5.1		2.6 4.0	31 49
Experiment 3. 7/28-8/7/61 (11 days)	2.1 2.1	5.9 ^{4/} 17.4 ^{4/}	4.0 9.8	3.5 6.1	69 71	96 126	86 123
Experiment 4. 8/20-9/4/61 (15.5 days)	2.1 2.0	5.9 ^{4/} 17.4 ^{4/}	4.0 9.7	3.5 5.9	84 72	112 135	101 131
Experiment 5. 9/23-10/8/61 (15 days)	1.9 2.0	8.3 ^{5/} 8.0 ^{6/}	4.0 6.0	3.1 5.0	83 99	122 157	101 142
Experiment 6. 10/19-11/3/61 (15 days)	3.8 1.8 1.8	24.1 ^{4/} 8.5 ^{5/} 8.1 ^{6/}	14.0 4.0 6.0	9.6 3.0 4.9	68 46 73	-- -- --	-- -- --

^{1/} The approximate mean oxygen concentrations shown are weighted means (arithmetic and geometric means weighted according to exposure time) of the mean low and mean high concentrations given in preceding columns.

^{2/} Actual weight gain of the fish subjected to fluctuating dissolved oxygen.

^{3/} Weight gain estimates were derived from the appropriate curves in Figure 3.

^{4/}, ^{5/}, ^{6/} See correspondingly numbered footnotes in Table 1.

at constant levels of dissolved oxygen equal to the arithmetic and geometric mean oxygen concentrations computed for each test with fluctuating dissolved oxygen. These values were obtained from the appropriate curves shown in Figure 3. No such values are given for experiment 6, because the curve in Figure 3 pertaining to this experiment does not closely fit all of the observations, and so is not deemed sufficiently reliable.

The approximate arithmetic and geometric mean oxygen concentrations given in Table 3 for test vessels with fluctuating concentrations are believed to be somewhat higher than the true mean concentrations. Arithmetic means based on eight series of dissolved oxygen determinations made every two hours in the course of 24-hour periods have been compared with approximate arithmetic means for the same 24-hour periods based only on the high and low concentrations that were usually determined. These data indicated that the latter means were, on the average, greater by about 3 percent than the true arithmetic means. Six of the 24-hour observations were made soon after the beginning and two near the conclusion of tests with fluctuating dissolved oxygen. The oxygen concentration in the test vessel usually approached the maximum or minimum level within about 4 to 5 hours after each change of the oxygen content of the influent water and remained more or less constant thereafter. This time interval evidently was somewhat longer when the oxygen concentration was being increased than when it was being reduced. The estimates of dry weight gains that would have occurred at constant oxygen concentrations equal to the mean concentrations

in vessels with fluctuating dissolved oxygen (Table 3) thus may be somewhat too high, as are probably the estimates of the concentration means. The likely error is believed to be negligible, however, as even a 5 percent difference of oxygen concentration would have only a slight or scarcely appreciable effect on growth (Figure 3).

The data in Table 3 show that the growth of bass subjected alternately to low and higher dissolved oxygen concentrations was markedly impaired. It was almost invariably less than the growth that presumably would have occurred had the fish been held at a constant concentration equal to the mean concentration (either the arithmetic or the geometric mean) of the water with fluctuating oxygen content to which they had been exposed. The data from experiments 5 and 6 (Table 3) further show that fish exposed for 8 hours of each day to relatively low oxygen concentrations and for 16 hours to higher concentrations grew more rapidly than did fish that were exposed for 16 hours of each day to the low concentrations and for 8 hours to the higher concentrations.

It is noteworthy that in all tests in which the fish gained weight and their initial and final lengths were determined, there was an improvement in the "condition" of the fish, as indicated by the ratio of weight to length. Condition indexes, $K(TL)$, (4, p. 8) based on the mean initial and final weights and total lengths of the fish have been computed according to the formula:

$$K(TL) = \frac{W 10^5}{L^3}$$

where W is the weight in grams and L is the total length in millimeters. Final condition indexes could not be determined for the fish used in experiment 3, because final lengths of the fish were not available. The increases in the condition index of the fish in the other experiments averaged about 11 percent at oxygen concentrations of 1.6 to 2.6 mg./l., 18 percent at concentrations of 3.0 to 4.2 mg./l., and 22 percent at concentrations near the air-saturation level (5.8 to 10.1 mg./l.). These increases apparently are not to be ascribable entirely to increases in average size of the fish. The mean initial condition indexes of the fish used in the first five experiments ranged from 1.07 to 1.13. Fish used in experiment 6 had a mean initial condition index of 1.25. These fish also exhibited the least increase in condition index. This result was to be expected, inasmuch as these fish apparently were in better condition initially than the fish used in the other five experiments. Not only the condition indexes, but also the ratios of dry weight to wet weight of growing fish tended to increase considerably in the course of experiments other than experiment 6. More complete data are given in Appendix Table A.

Food Consumption and Food Conversion

Figure 4 shows the average food consumption rate, in grams of food consumed per day per gram of initial body weight, of juvenile

largemouth bass held at various dissolved oxygen concentrations. A curve fitted by eye to the plotted points is shown for each experiment. The curve pertaining to experiment 6 was drawn in the same manner as the corresponding curve in Figure 3. The curves in Figure 4 show that the effects of oxygen concentrations on food consumption rates are similar to the effects on growth (Figure 3). The observed differences in growth of the bass at different oxygen concentrations appear to be closely associated with differences in appetite.

Figure 5 shows the relation between oxygen concentrations and food conversion ratios, or gross conversion efficiencies (3, p. 386). The conversion ratio for the fish held at a mean oxygen concentration of 1.7 mg./l. in experiment 2 was considered to be zero in plotting the data, because these fish lost weight and a negative conversion ratio is not considered to be meaningful. The curve pertaining to experiment 6 was once again drawn in Figure 5 (as in Figure 3) to correspond in shape to the curve for experiment 3, disregarding the anomalous observations made at the oxygen concentration of 8.1 mg./l. The data plotted in Figure 5 show that the gross food conversion efficiency was considerably reduced at oxygen concentrations well below 4 mg./l. However, the gross food conversion efficiency does not increase very much with increase of oxygen concentration beyond 4 mg./l. A slight reduction of food conversion efficiency may have occurred at oxygen concentrations far above the air-saturation level.

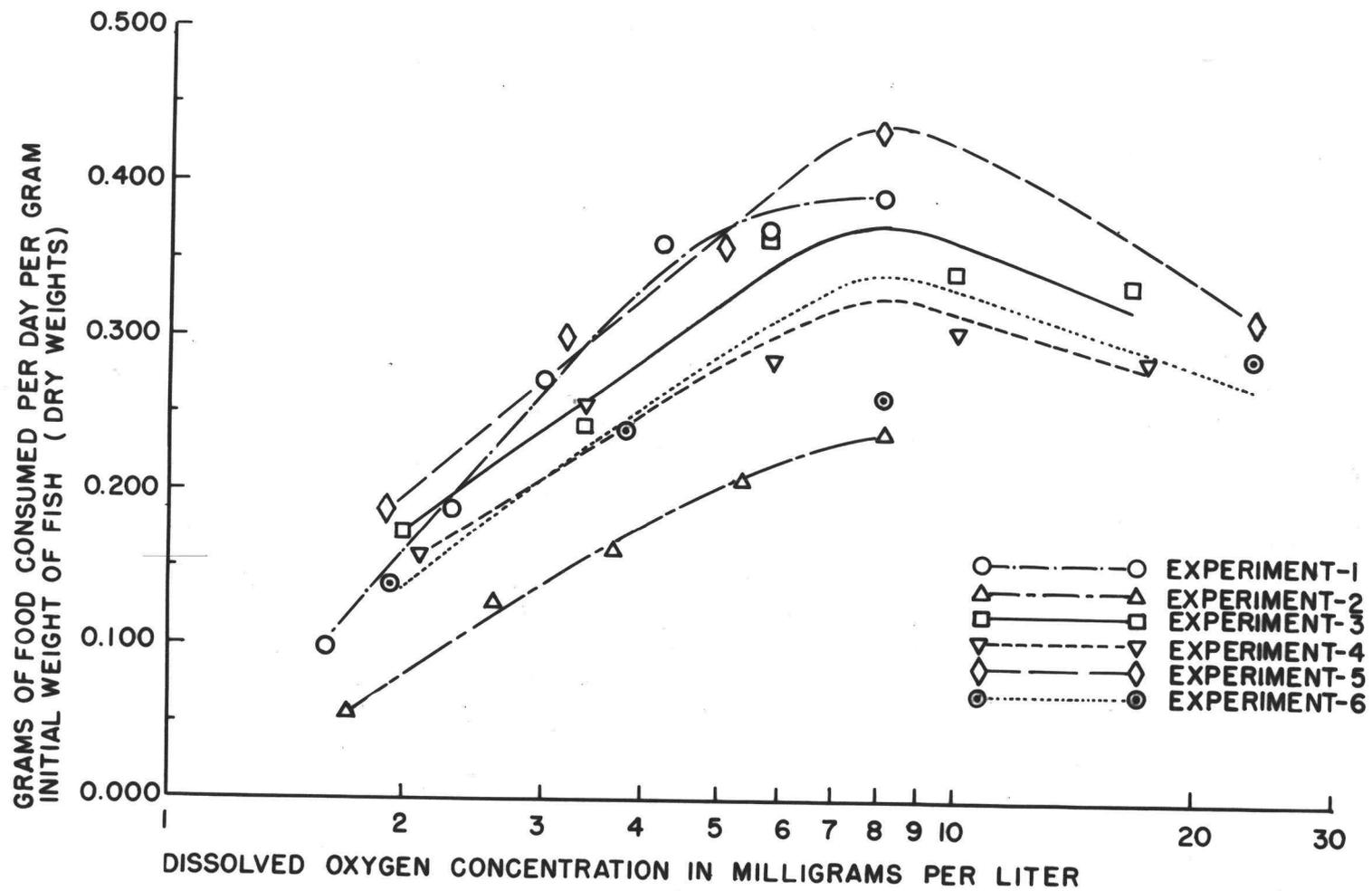


Figure 4. Grams of food consumed per day per gram initial weight of largemouth bass, in relation to dissolved oxygen concentration.

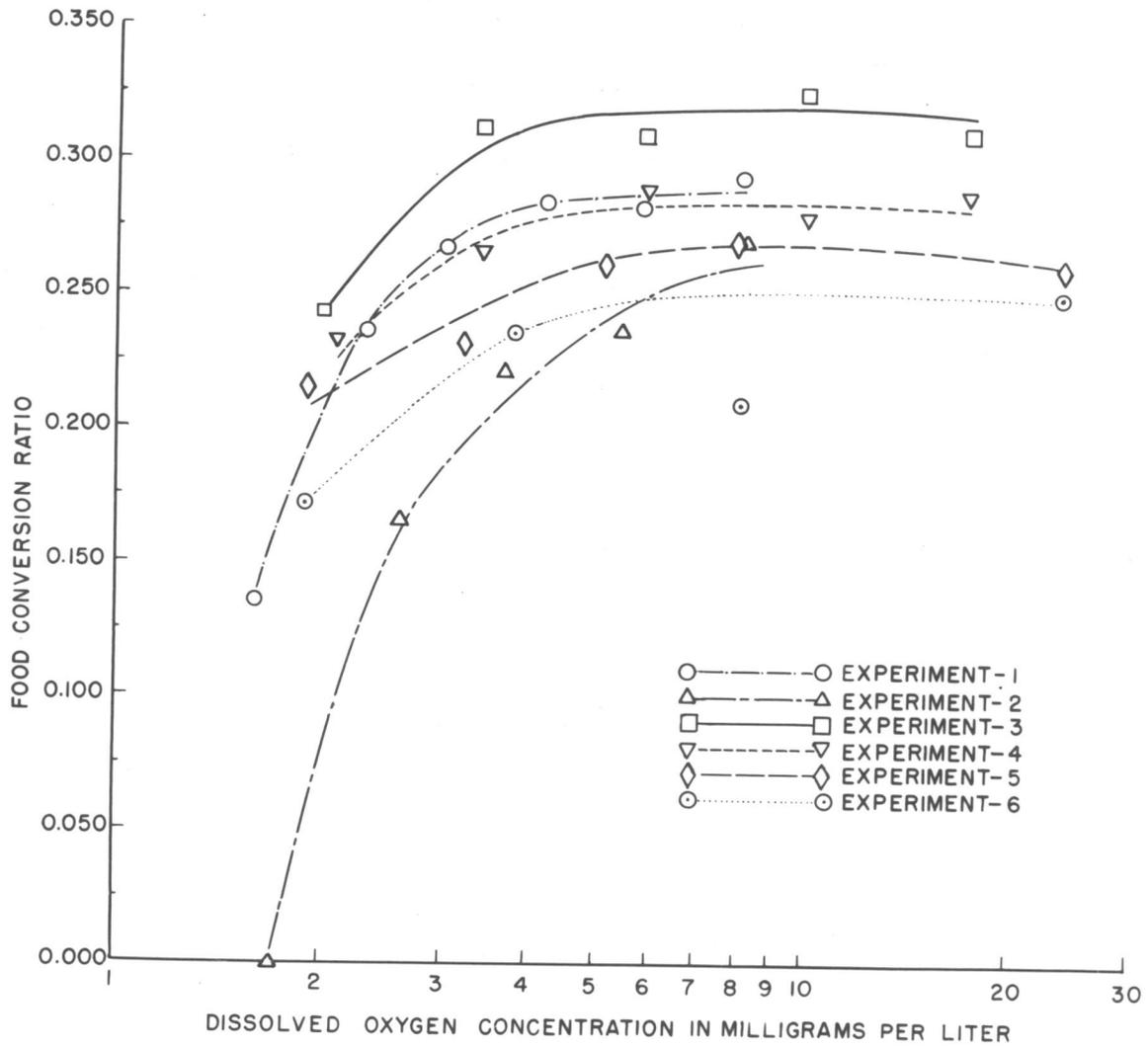


Figure 5. Food conversion ratios in relation to dissolved oxygen concentration. The food conversion ratio of those fish that lost weight was considered to be zero, regardless of the weight loss.

It should be noted that only the shapes and not the relative position of the individual curves shown in Figures 4 and 5 can be meaningfully compared. As explained earlier, the dry weight of food consumed in all experiments was computed by using a common factor based on the mean "percent dry weight" of the food (17 percent) that was determined from various samples of food (earthworms) taken at different times during the course of the experiments. Consequently, the computed food consumption values probably are high for some experiments and low for other experiments. Thus, the relative positions of the curves in Figures 4 and 5 probably would have been somewhat different had the ratio of dry weight to wet weight of the consumed food been determined accurately for each individual experiment. Inasmuch as an undetermined portion of the dry or wet weight of at least some of the worms is referable to the weight of residual contents of their alimentary tracts, of little or no nutritional value for fish, the food consumption and conversion efficiency values reported have limited significance. However, results obtained in any one experiment with food of uniform quality, are deemed entirely comparable, and the relationships between them are certainly meaningful.

DISCUSSION

Herrmann, Warren, and Doudoroff (11, p. 166) have reported that both the percent gains in weight and the food consumption rates of juvenile coho salmon at 20° C. declined slightly with reduction of oxygen concentration from 8.3 to 6 and 5 mg./l. The growth and food consumption rates declined more sharply with further reduction of oxygen concentration. In other words, equal differences of oxygen concentration had much greater effect when the concentrations were well below 5 mg./l. than when the concentrations were above 5 mg./l. Most of the curves in Figures 3 and 4 show more nearly uniform decreases in growth and food consumption rates of largemouth bass (at 26° C.) with equal decreases of oxygen concentration between a level slightly below air-saturation (7 to 8 mg./l.) and a level near 2 mg./l. However, the results of all experiments in which concentrations above the saturation level were tested, except for the anomalous results of experiment 6, indicate a more or less abrupt decline of growth and food consumption rates of the bass with increases of oxygen concentration beyond the saturation level. No comparable data are available on the effect of supersaturation levels of dissolved oxygen on growth of coho salmon.

As can be seen in Figure 3, there was a large variance in the growth rates of fish tested at similar oxygen concentrations in different experiments, and the curves representing results of the different experiments are not parallel. No apparent correlation was

found between the initial size or the initial condition indexes of the fish and the observed growth rates. Also, there was no apparent correlation of growth rate with the season of the year. Genetic differences of the fish obtained from different sources may possibly have been responsible for some of the differences in results of the different experiments. However, the fish used in experiments 3 and 4, which were performed at about the same time of year, came from the same source, and their growth rates apparently were still quite different. As can be seen in Figure 3, the fish tested in experiment 3 grew in 11 days almost as much as the fish tested in experiment 4 grew in 15.5 days. Had experiment 3 been continued for 15.5 days, the percent weight gains of the fish at oxygen concentrations near the air-saturation level presumably would have been much greater than those which were observed in experiment 4, and perhaps even greater than that which was observed at the saturation level in experiment 5. With the small amount of data available, it is impossible to determine just what were the factors contributing to the large variance in growth of fish in the different experiments.

The reason for the reduced growth of fish held at oxygen concentrations well above the air-saturation level, as compared to growth of fish held at concentrations near the air-saturation level, is uncertain. Doudoroff (8, p. 415-416) has pointed out that "Supersaturation of water with atmospheric gases (chiefly nitrogen and oxygen) can cause fatal 'gas-bubble disease' of fish when the total pressure of the dissolved gases (i.e. the sum of their individual

tensions) greatly exceeds the hydrostatic pressure, including the pressure of the atmosphere." He also states that, "Mere bubbling of pure nitrogen or oxygen through water, which drives out one gas and substitutes another without increasing the total gas tension, evidently cannot cause the disease." The high oxygen concentrations tested in this study were produced by bubbling oxygen gas through the water. There was no evidence of gas-bubble disease having occurred at any high level of oxygen tested, even though the total tension of the dissolved gases (mainly oxygen and nitrogen) in the water may have slightly exceeded the sum of the hydrostatic and atmospheric pressures. Apparently some other factor or factors were responsible for the inhibition of the growth of fish held at oxygen concentrations well above the air-saturation level.

West and Todd (16, p. 595-596) have discussed the toxicity of high oxygen concentrations to warm-blooded animals. These authors have pointed out that one effect of breathing oxygen at very high partial pressures is an impairment of carbon dioxide transport by the blood, which results in an excess of carbon dioxide in the intracellular and extracellular fluids of the body and an associated decrease of their pH. Other workers have expressed the opinion that the toxicity of high pressures of oxygen may be brought about by more direct, oxidative destruction or inhibition of some enzyme systems (14, p. 111). Dickens (7, p. 184) reported that certain enzymes of rat brain tissue, which are believed to be involved in carbohydrate metabolism, are capable of being inhibited by oxygen.

One or both of the above-mentioned effects of high oxygen pressures may possibly occur in fish also, and may have contributed to the impairment of appetite and growth of juvenile bass held at abnormally high oxygen tensions.

It is interesting to note that Davis (5, p. 18-34) found that the maximum sustained swimming speed of juvenile coho salmon at 12° and 15° C. was not reduced at oxygen concentrations somewhat in excess of 200 percent of air-saturation.

The food conversion ratios (gross food conversion efficiencies) of largemouth bass were considerably reduced at concentrations well below 4 mg./l. Reduced oxygen concentrations above 4 mg./l. had very little effect on food conversion ratios. Similar results have been obtained with coho salmon (11, p. 162). Some reduction in gross food conversion efficiency at low oxygen concentrations can be expected because of the low food consumption rates observed at the low concentrations (Figure 4). As the fish eat less food a larger percentage of the food eaten is needed for satisfying a nearly constant maintenance requirement and less is available for growth. It has been pointed out that digestion or assimilation of food by silver salmon may possibly be impaired at very low oxygen concentrations (11, p. 166). Such impairment also would result in reduced food conversion efficiency at low oxygen concentrations. The relatively small decline in food conversion ratios observed at moderately reduced oxygen concentrations above 4 mg./l. may be explained in part by a decrease in activity of the fish at these oxygen concentrations.

This would result in a decrease of the overall maintenance requirements of the fish. Furthermore, digestive and assimilatory efficiency may well improve with some reduction of the rate of ingestion of food. Reduction of maintenance food requirements (due to reduction of activity) and improvement of digestive efficiency both would tend to make possible unimpaired gross food conversion efficiency at the moderately reduced oxygen concentrations at which food consumption rates are not too greatly reduced. The data plotted in Figure 5 indicate that a slight reduction in food conversion ratios may have occurred at oxygen concentrations well above the air-saturation level, at which the food consumption rates of the fish also were usually reduced, as compared with rates observed at concentrations near the air-saturation level.

The observed adverse effect of diurnally fluctuating oxygen concentrations on the growth of largemouth bass appears to be an important factor to be considered in defining a favorable environment for fishes. Regulatory agencies concerned with water pollution control usually have prescribed only single, minimal limits of dissolved oxygen concentrations considered to be necessary for sustaining well-rounded warm-water fish populations. The Aquatic Life Advisory Committee of the Ohio River Valley Water Sanitation Commission (2, p. 327), on the other hand, has suggested that dissolved oxygen concentrations in suitably protected warm-water fish habitats 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. The results of the

present investigation indicate that even when oxygen concentrations are near 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. They also show that the occurrence of exceedingly high 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. It is evident that, as suggested by Tarzwell and Gaufin (15, p. 309), averages of dissolved oxygen concentrations determined at different times of day are by themselves almost useless as indexes of the suitability for fish of dissolved oxygen conditions in aquatic environments. Both minimum and maximum levels, and also the duration of persistence of low and high concentrations, evidently must be considered in evaluating fish habitats and the adverse effects of organic pollution.

The manner which the food consumption and growth rates of bass were affected by cyclic fluctuations of oxygen concentration is not yet clearly understood. Before an explanation is attempted, additional experiments should be undertaken to determine how and to what extent these effects may be influenced by varying the timing of the increases and decreases of oxygen concentrations, the conditions of illumination, etc. The relative amounts of food consumed during the

exposures to the alternating low and higher concentrations, and the possible influence of oxygen concentration on the rate of digestion also should be evaluated.

The influence of oxygen concentration on the food consumption and growth rates of largemouth bass under natural conditions may be very different from that observed under the experimental conditions in the laboratory. In the laboratory experiments, the food supply was unrestricted, and the fish did not grow as well at any reduced oxygen concentrations as they did at concentrations near saturation, because the amount of food that they were able to utilize was limited by the amount of available oxygen. In nature, food is not always readily available, and the availability of food often may be the principal factor limiting the rate of growth. If food is limiting in nature, largemouth bass might conceivably grow about as well at some reduced oxygen concentrations as at higher concentrations in otherwise identical natural environments, because even at the reduced concentrations they might still capture, digest, and assimilate as much food as could be obtained.

However, Herrmann, Warren, and Doudoroff (11, p. 167) have pointed out, fish in nature may have to be much more active in seeking and pursuing their prey than they need to be under the laboratory conditions. If this be true, much more of the oxygen that fish are able to extract from their medium at any given concentration may be required for the maintenance of necessary activity in nature than in the laboratory, and at reduced concentrations in nature very

little oxygen may be available for digestion and assimilation of food. Thus, normally active fish in nature may be unable to consume at the reduced oxygen concentrations even a limited amount of food that would be consumed at higher concentrations. Yet, any compensatory reduction of activity presumably would interfere with the search for food and its capture. Thus, growth may be even more seriously impaired at a given reduced oxygen concentration in nature than it was found to be under the experimental conditions. The fairly rapid growth of bass observed at oxygen concentrations near 2 mg./l. in most of the laboratory experiments reported may not be very different from that occurring frequently in nature under more favorable dissolved oxygen conditions, and the calculated condition indexes of these bass remained undiminished or even increased. For the reason indicated above, it cannot be assumed that bass could grow nearly as well and remain in good condition at oxygen concentrations near 2 mg./l. in nature, in the presence of an available supply of food that would be adequate at higher concentrations.

SUMMARY

1. Six laboratory experiments were performed to determine the influence of nearly constant oxygen concentrations both below and above the air-saturation level, and also of diurnal fluctuations of oxygen concentration, on the growth, food consumption, and food conversion efficiency of juvenile largemouth bass, Micropterus salmoides (Lacépède), kept on an unrestricted diet of live earthworms. The experiments were usually 15 days in duration and were performed at temperatures near 26° C. during the period from April to November, 1961.
2. The experimental apparatus used was designed to provide constant flows of water of uniform temperature and controlled oxygen content through 12-gallon bottles containing the test fish. The desired oxygen concentrations were maintained by bubbling either nitrogen or oxygen gas through the water before it entered the test vessels.
3. In all experiments except one, the growth rates of bass increased markedly as the oxygen concentration increased up to levels near the air-saturation level. The growth rates usually declined with further increase of oxygen concentration well beyond the air-saturation level.
4. The growth of bass subjected alternately to low and higher dissolved oxygen concentrations was markedly impaired. It was almost invariably less than that which presumably would have occurred had the fish been held at a constant concentration equal to the

mean concentration (either the arithmetic or the geometric mean) in the water with fluctuating oxygen content to which they had been exposed.

5. The effects of oxygen concentration on food consumption rates of largemouth bass were similar to the effects on growth. The differences in the growth rates of bass at different oxygen concentrations appear to be closely associated with differences in food consumption.

6. Gross food conversion efficiencies were considerably reduced at oxygen concentrations well below 4 mg./l. Efficiencies observed at different oxygen concentrations above 4 mg./l. did not differ markedly.

7. The physiological and ecological significance of the experimental results is discussed.

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APPENDIX

TABLE A

Mean Lengths, Condition Indexes, and "Percent Dry Weights"^{1/} of Surviving Largemouth Bass Tested at Various Oxygen Concentrations

Experiment Number and Mean Oxygen Concentration (mg./l.)	Mean Test Temperature (°C.)	Mean Total Length of Fish (mm.)		Mean Condition Index of Fish		Percent Increase in Condition Index	Mean "Percent Dry Weight" of Fish ^{1/}	
		Initial	Final	Initial	Final		Initial ^{2/}	Final
Experiment 1.								
1.6	25.0	62.2	62.1	1.03	1.19	16	22.3	23.2
2.3	25.1	61.8	68.4	1.09	1.29	18	"	23.1
3.0	25.2	61.7	72.4	1.13	1.36	20	"	23.9
4.2	—	61.0	75.0	1.09	1.38	27	"	23.8
5.8	25.1	63.1	76.1	1.08	1.47	36	"	23.8
8.1	25.1	61.1	76.3	1.08	1.40	30	"	24.2
Experiment 2.								
1.7	25.9	85.0 ^{3/}	82.3	1.07	1.09	2	23.6	23.9
2.6	25.9	82.2	85.7	1.10	1.26	15	"	24.0
3.7	26.0	85.5	91.9	1.10	1.32	20	"	24.3
5.4	—	85.7	96.4	1.10	1.28	16	"	24.5
8.2	26.0	85.9	99.5	1.11	1.35	22	"	24.5
1.8-3.7 ^{4/}	26.0	82.5	86.7	1.13	1.24	10	"	24.4
1.9-8.3 ^{4/}	—	85.4	92.3	1.10	1.26	15	"	24.5
Experiment 3.								
2.0	26.0	68.5	—	1.07	—	—	22.0	21.3
3.4	26.0	67.5 ^{3/}	—	1.12	—	—	"	22.1
5.9	—	65.3	—	1.12	—	—	"	22.0
10.0	26.0	65.7	—	1.13	—	—	"	23.3
17.5	26.0	65.1	—	1.18	—	—	"	23.1
2.1-5.9 ^{4/}	26.0	66.5	—	1.15	—	—	"	21.3
2.1-17.4 ^{4/}	—	66.9	—	1.14	—	—	"	21.8
Experiment 4.								
2.1	26.1	67.7	76.2	1.08	1.17	8	22.6	22.9
3.4	—	68.4	82.8	1.07	1.23	15	"	22.5
5.9	26.1	69.3	85.4	1.06	1.25	18	"	23.3
10.1	26.0	67.5	84.0	1.09	1.27	17	"	23.3
17.5	26.1	68.0	83.9	1.07	1.25	17	"	23.5
2.1-5.9 ^{4/}	26.1	67.5	79.7	1.08	1.19	10	"	22.8
2.0-17.4 ^{4/}	—	68.7	80.8	1.07	1.13	6	"	22.9
Experiment 5.								
1.9	25.7	73.8	80.0	1.04	1.22	17	22.3	23.8
3.2	25.8	73.3	86.7	1.11	1.28	15	"	23.9
5.1	—	72.8	88.3	1.05	1.31	25	"	24.3
8.0	25.8	73.4	92.7	1.08	1.35	25	"	24.5
24.1	25.8	73.2	87.0	1.05	1.26	20	"	24.6
1.9-8.3 ^{5/}	—	72.2	82.4	1.09	1.26	16	"	23.8
2.0-8.0 ^{6/}	25.8	73.7	86.4	1.10	1.27	15	"	24.0
Experiment 6.								
1.9	—	64.5	71.5	1.26	1.27	1	24.7	24.5
3.8	25.6	64.0	76.4	1.24	1.37	10	"	24.1
8.1	25.6	64.1	77.9	1.21	1.26	4	"	24.1
23.8	25.5	64.7	79.7	1.23	1.36	11	"	24.7
3.8-24.1 ^{4/}	—	64.2	75.6	1.24	1.31	6	"	24.0
1.8-8.5 ^{5/}	25.5	63.8	72.4	1.26	1.28	2	"	24.1
1.8-8.1 ^{6/}	25.6	64.5	76.4	1.28	1.35	5	"	24.3

- ^{1/} The "percent dry weight" is the dry weight expressed as a percentage of the wet weight.
^{2/} The initial percent dry weight was computed by using a ratio of dry weight to wet weight determined from a sample of 10 fish taken at the beginning of each experiment.
^{3/} Mean initial length of all fish used in test. Inasmuch as one fish died during the experiment and its initial length and weight could not be determined, this may not be the correct initial mean length of surviving fish. Consequently, the initial condition index and the percent increase in condition index reported for the same test may be also slightly in error.