

AN ABSTRACT OF THE THESIS OF

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Title: INFLUENCE OF DISSOLVED OXYGEN AND TEMPERATURE
ON THE GROWTH OF JUVENILE LARGEMOUTH BASS HELD
IN ARTIFICIAL PONDS

Abstract approved: _____

Redacted for privacy

Mr. Dean L. Shanway

The food consumption and growth of actively foraging largemouth bass, Micropterus salmoides, were studied in artificial ponds maintained at various temperatures and dissolved oxygen concentrations. The study was conducted at the Oak Creek Fisheries Laboratory of the Department of Fisheries and Wildlife, Oregon State University, during 1970 and 1971.

The food consumption and growth of juvenile largemouth bass were determined for 2-week experiments during which four bass were allowed to forage on moderate densities of mosquitofish, Gambusia affinis, in each of two experimental ponds simultaneously. The dissolved oxygen concentration of one pond was maintained near the air-saturation level, and that of the other pond was reduced to concentrations of 4 to 6 mg/liter. The temperature, held near the same level in both ponds, ranged from 13 to 27 C.

Results of these experiments show that the food consumption and growth rates of juvenile largemouth bass maintained in the experimental ponds on moderate densities of forage fish increased with temperature, and decreased with moderate reductions of dissolved oxygen below the air-saturation level, except at low temperatures. The total metabolic rate estimated for the largemouth bass reared in the ponds was limited by the reduction of dissolved oxygen, except at low temperatures.

Influence of Dissolved Oxygen and Temperature on the Growth
of Juvenile Largemouth Bass Held in Artificial Ponds

by

Lynn Albert Brake

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INFLUENCE OF DISSOLVED OXYGEN AND TEMPERATURE
ON THE GROWTH OF JUVENILE LARGEMOUTH BASS
HELD IN ARTIFICIAL PONDS

INTRODUCTION

In nature many factors including food, temperature, turbidity, toxicants and dissolved oxygen may limit the abundance, distribution, and production of freshwater fish. Since the addition of any putrescible organic waste to surface waters may cause a reduction in the dissolved oxygen concentration, the oxygen factor of water quality is of general concern and a very widely studied water pollution problem. Ellis (1937) in his classical study on the detection of stream pollution, determined the dissolved oxygen concentration, and fish faunas in numerous freshwater streams in different regions of the United States. He concluded that in many locations the dissolved oxygen concentration of the water was an important factor limiting the abundance and distribution of many species of fish.

In recent years, many studies have been conducted on the effect of oxygen deficiency on the metabolism, growth, development, locomotion, and behavior of various species of fish and other aquatic organisms. Several summaries including many of these studies and discussions of the practical significance of these data have been published during the past decade (Fry 1960; Jones 1964; Doudoroff and Warren, 1965). More recently Doudoroff and Shumway (1970) have

completed a comprehensive and detailed treatise that deals quite extensively with many aspects of the effect of dissolved oxygen variation on freshwater fish. The ultimate goal of the study of oxygen requirements of fish must be to determine what levels of dissolved oxygen are necessary to protect the production of valuable species in natural systems.

Once fish have hatched successfully, one of the major factors that determines the yield (man's harvest) of a fishery is the elaboration of new tissue (growth) by individual fish within the population. Production is the total tissue elaboration by all the fish in a population. The rate of production must be calculated for each age group of a fish species separately, and can be determined by multiplying the biomass of each age group by the mean growth rate for that group. Environmental factors which effect the growth of individual fish can be expected to effect production. As Shumway and Doudoroff (1970) point out, even a small depression of growth rate that reduces the efficiency at which juvenile fish are able to utilize the available food source can have a serious effect on overall production. It is very difficult to accurately measure the production in natural systems and to isolate the effect of any one of the many uncontrolled variables, so most of the understanding we have of the oxygen requirements of fish has come through laboratory studies.

The results of laboratory studies performed in the past using many types of controlled environments have provided a good basic understanding of the relationship between dissolved oxygen concentration and the growth of fish. The following is a brief summary of conclusions common to many of the studies. Any substantial reduction in oxygen below the air saturation level can materially restrict the growth of rapidly growing fish fed to excess in laboratory aquaria (Herrmann, Warren, and Doudoroff, 1962; Stewart, Shumway, Doudoroff, 1967; and Trent, 1971). Fish growing more slowly due to restricted rations, unfavorable temperatures, nutritionally deficient or unattractive food, or other factors which reduce consumption will be less effected by the reduction of oxygen levels (Fisher, 1963; and Trent, 1971). Fish fed unrestricted rations and forced to swim against a current consume less food and grow less as swimming speed increases (Hutchins 1970). Increases in temperature results in increased food consumption and growth rates of fish fed both restricted and unrestricted rations (Lee 1969; Brown 1946; Swift 1955).

The usefulness of laboratory data in predicting the effect of reduced dissolved oxygen concentrations on the production of fish may be limited unless a relationship between the metabolism and growth of fish in nature and in the laboratory can be demonstrated. The study reported here was designed to test the effect of temperature

and reduced dissolved oxygen concentration on the food consumption and growth of largemouth bass, Micropterus salmoides, allowed to forage on mosquitofish, Gambusia affinis, in a nearly natural predator-prey relationship. The experiments were conducted in small artificial ponds in which the temperature, dissolved oxygen concentration, food availability, and bass density could be controlled.

EXPERIMENTAL ANIMALS

The largemouth bass used in these experiments were seined from a pond near Jefferson, Oregon. The fish were graded according to size and only those up to 120 mm in length were selected. The bass were transported to the Oak Creek Laboratory and were placed in 190-liter glass aquaria held near 18 C. During this holding period, the bass were fed live mosquitofish.

The mosquitofish used as food for the bass were collected from several small log ponds in the local area. It was necessary to collect mosquitofish from more than one source because of limited abundance and because the fish in some areas became diseased as the water fell to a low level in the late summer. After transportation to the laboratory, the mosquitofish were held outdoors in a wooden tank equipped with a 2000 watt stainless-steel immersion heater and were fed Oregon moist pellets.

Experimental Apparatus

Two oval, concrete-lined experimental ponds, approximately 6 m in diameter and with a capacity of about 19,000 liters were used in this study. From a shallow peripheral area, the bottom of each pond slopes sharply to a central area, where the depth is about 1 meter (Figure 1). A wooden rectangular observation chamber with

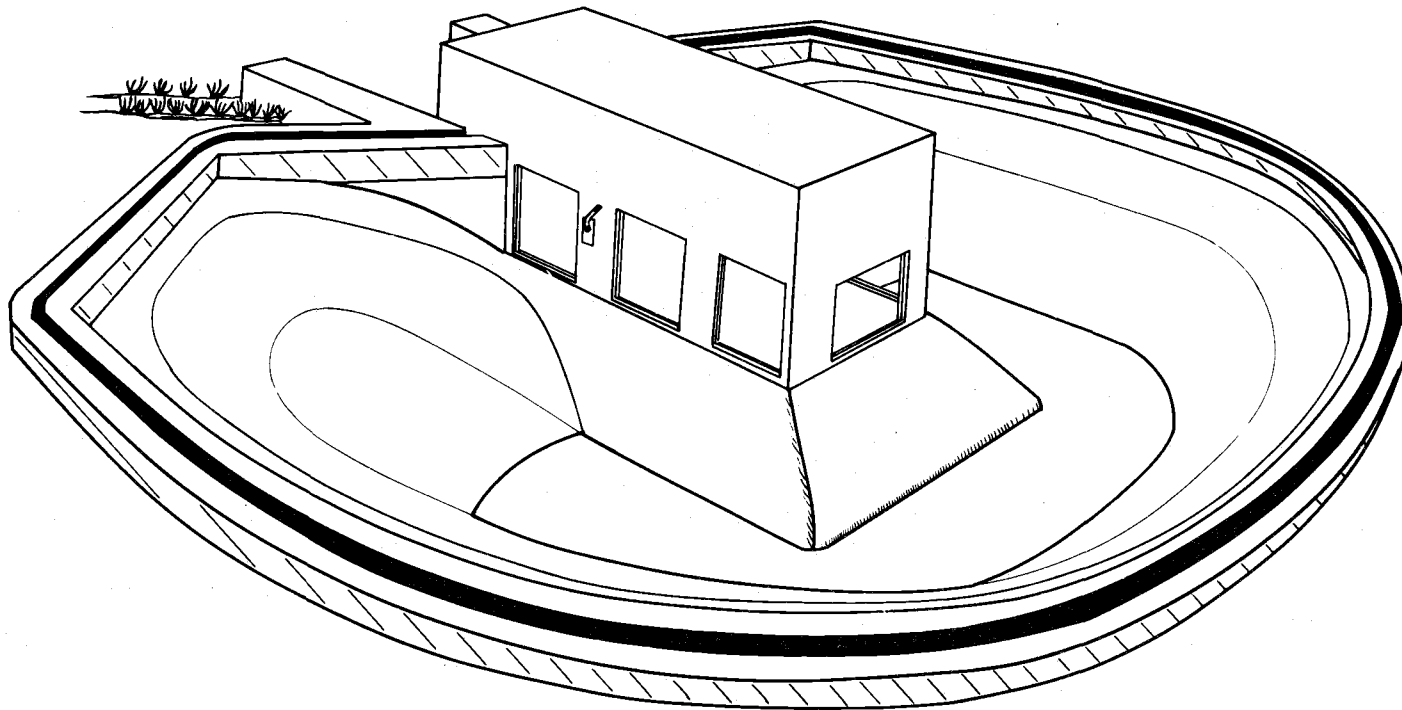


Figure 1. Schematic drawing of one of the two experimental ponds used in this study. Each pond was equipped with an observation chamber and an adjustable standpipe to maintain the desired water level in the pond.

seven underwater glass ports projects to near the center of each pond. The observation chambers and cracks which occurred in the concrete were covered with fiberglass to prevent the leakage of water and to protect the wooden chambers from deterioration. Cylinders constructed of chickenwire and painted with non-toxic paint were placed end to end around the shallow periphery of the ponds to provide escape cover for the mosquitofish. These ponds are described in detail by Lee (1969).

Each pond was fitted with a transparent polyethelene cover sealed to the edge of the pond by a water seal and supported by a frame made of aluminum conduit (Figure 2). The cover sloped from the water seal at the edge of the pond to a height of 1 m from the water surface in the center. The sealed cover prevented the entry of unwanted food organisms, and made it possible to maintain a low oxygen atmosphere above the ponds which slowed reoxygenation. Small wooden doors on both sides of the observation chamber slightly above the water level provided access to the pond beneath the plastic cover.

Both ponds were equipped with air lines supplying five dispersion stones which were distributed evenly around the bottom of the pond and through which nitrogen or air could be forced. Introduction of oxygen or nitrogen through the stones promoted mixing of the water and helped to maintain the desired dissolved oxygen level.

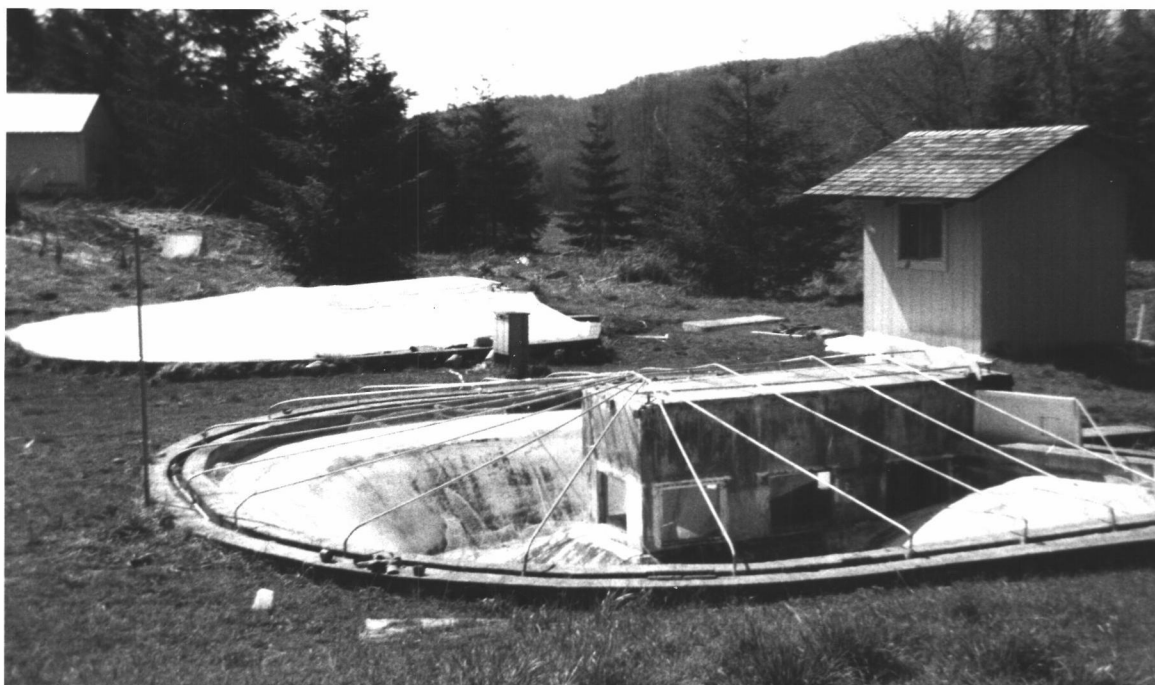


Figure 2. The experimental ponds used in this study shown with and without the plastic cover.

The temperature of each pond was maintained by two 2000-watt stainless-steel immersion heaters controlled by thermoregulators. The water temperature was monitored with a continuously recording thermograph.

The well water in the ponds was renewed continuously through separate flowmeters at a rate of 4 to 10 liters/min. The flow rate was adjusted as necessary for maintaining the desired dissolved oxygen level and water temperature.

The water delivered to one of the ponds passed through a degasser, an apparatus designed by Mount (1964) to remove dissolved gases from water. Once in the degasser, water is circulated by a pump through a vacuum chamber where the gases come out of solution and are removed continuously with a vacuum pump. A mixture of renewal and recycled pond water passed through the degasser at a rate of 15 to 25 liters/min. The water flow through the degasser and the vacuum were adjusted to produce the desired dissolved oxygen concentration in the experimental pond.

To maintain the desired dissolved oxygen concentration in the pond, it was necessary to make several modifications in the degasser as described by Mount (1964). Adequate reduction of dissolved oxygen concentration of the large volume of water as it circulated through the degasser required a larger volume vacuum pump (79 liters/min) and a larger diameter (13 mm) vacuum hose

between the vacuum pump and the vacuum chamber. To keep water vapor from being drawn from the vacuum chamber into the vacuum pump, a dessication column constructed of a stoppered 1 m length of 5 cm plexiglass tubing filled with silica gel was installed in the vacuum line. The silica gel was changed periodically as it became saturated with water.

Occasionally the water pump failed, allowing the vacuum chamber to fill with water which was pulled through the vacuum pump resulting in damage to the pump. To prevent reverse water flow when the water pump failed, check valves were placed in the influent and effluent water pipes. Additionally, the electrodes of a high-level, shut-off relay were installed in the vacuum chamber to shut off the vacuum pump if the chamber filled with water. The addition of the shut-off relay made it necessary to install a check valve in the vacuum line to prevent the negative pressure from drawing pump oil into the dessication column when the vacuum pump was stopped with the chamber under vacuum. With the above modifications, the degasser system operated with a minimum of trouble and maintenance.

Experimental Procedures

In this study, an experiment is defined as a 14-day test during which bass were maintained in both experimental ponds simultaneously on equal weights of mosquitofish. During each experiment the dissolved oxygen concentration of the water in one pond was maintained at the air-saturation level, while that of the other was reduced to a desired level. An attempt was made to avoid any other differences in test conditions such as temperature, water level, exchange rate, etc. Several days before the start of an experiment, the ponds were filled with water and regulated to the desired test conditions.

Once the test conditions had been established in each pond, an appropriate number of mosquitofish of fairly uniform size were selected from the available stock, discarding the largest and smallest individuals and those that appeared unhealthy or were in late stages of pregnancy. After an adequate quantity of mosquitofish had been selected, one of two techniques were used to select samples of the mosquitofish before each experiment. In experiments 1, 2, 3, and 7, samples of mosquitofish weighing 5 g each were sacrificed, dried to a constant weight in an oven at 70 C, and then reweighed to obtain dry weights. In the remainder of the experiments, samples consisting of 50 mosquitofish were selected at random and handled in the manner described above.

The desired weight of mosquitofish was stocked in the ponds 2 days before the beginning of each experiment to allow them to become oriented before the bass were introduced. Normally, 170 g of mosquitofish were placed in each pond, but in experiment 6 and 7 the initial prey densities were 100 and 240 g/pond, respectively. The quantity of mosquitofish in the ponds decreased as they were consumed by the bass. No attempt was made to replace forage fish eaten during the test period, because it was observed that mosquitofish recently placed in the pond were disoriented initially and easily captured by the bass, thus upsetting the more natural prey-predator relationship previously established. The prey density was thus permitted to decrease during the experiment, sometimes to about one-half of the initial level.

Since the experimental ponds contained little or no food for the mosquitofish, a small quantity of a dry commercial guppy food was fed at a rate estimated to be a maintenance ration (i. e., ration that would allow neither weight gain or loss during the experimental period).

Several days before the start of each experiment, 10 bass of similar size were selected from the available stock, individually marked with the cold-brand techniques as described by Groves and Novotny (1965), and then returned to a 190-liter aquarium and held at the temperature to be maintained in the ponds in the ensuing

experiment. At the start of the experiment, the marked bass were individually weighed and measured, and four bass were placed into each experimental pond. The bass were selected to provide about the same total weight in each pond. The two remaining bass were sacrificed and dried to a constant weight in an oven at about 70 C.

During the experiments, the apparatus was checked twice daily, and when necessary, adjustments were made in the temperature, dissolved oxygen concentration, and water level in the ponds. The dissolved oxygen concentration in each pond was determined at least twice daily using the azide modification of the iodometric method (American Public Health Association, et al., 1965). Adjustments of the dissolved oxygen concentration in the pond were made by changing the amount of nitrogen being dispersed through the water, by adjusting the amount of vacuum in the degasser, or by changing the amount of water circulating through the degasser.

When each experiment was terminated, the bass and remaining mosquitofish were removed from the ponds. The bass were identified according to their marks, individually weighed, measured, sacrificed, and dried to a constant weight. The mosquitofish were weighed in aggregate and samples were taken and processed in the manner described above.

In every experiment both planktonic and filamentous algae grew much faster in the pond held at the reduced oxygen level than

in the pond held at the air-saturation level. Although the exact cause of the difference in the growth rates of algae in the two ponds is not known, it may have been due to the difference in oxygen concentrations. Gibbs (1970) reported that in many kinds of plants, including algae, the production of usable photosynthate is measurably reduced in the presence of normal oxygen concentrations. Growth reportedly increased as the level of oxygen in the plant's environment decreased.

The oxygen produced by the algae during photosynthesis caused large diurnal fluctuations in the dissolved oxygen concentration of the water in the pond which made it difficult to maintain a reduced oxygen level. The algae may also have effected the food availability balance between the two ponds by reducing the visibility more in the pond with the heaviest algae growth. To control the algal growth, both ponds were treated with an 80% preparation of simizine (2-chloro-4,6-bis [ethylamino]-s-triazine) at a concentration of 3 ppm. The ponds were treated with simizine during each of the experiments, except experiment 1. Normally, the excessive algae growth was controlled by one treatment near the beginning of each experiment, but two treatments were required for experiments conducted during the late summer months.

RESULTS

Results of this investigation show that the food consumption and growth rates of juvenile largemouth bass reared in experimental ponds and provided with a moderate density of food increased with temperature and decreased with moderate reductions of dissolved oxygen concentration below the air-saturation level, except at low temperatures. Table 1 lists the mean initial and final weights, mean growth rates and food consumption rates of the largemouth bass held for two weeks in the experimental ponds. The mean temperatures and dissolved oxygen concentrations at which the ponds were maintained during each experiment are also given in Table 1. The individual lengths, weights, growth rates, and caloric values of the largemouth bass, and the ranges of temperature and dissolved oxygen are recorded for each experiment in Appendix I. The growth of bass during the experiments was determined by direct measurement; food consumption was estimated from the change in mosquitofish biomass during the experiment.

The weight gained by bass held in the experimental ponds was determined by calculating the difference in the initial and final weights of each bass. The growth values were converted to rate terms to provide a basis for comparison between experiments. In this study, growth rates are expressed in terms of milligrams of weight gained per gram of mean weight of bass per day ($\text{mg}/\bar{g}/\text{day}$). The rate of

Table 1. Mean dissolved oxygen concentrations and temperatures and initial prey densities to which juvenile largemouth bass were subjected in the pond experiments. The mean initial and final weight, mean growth rates, and food consumption rates for bass held in the ponds. Four bass were held in each pond.

Experiment No. and date	Mean dissolved oxygen (mg/liter)	Mean temp. (C)	Initial prey density (g/pond)	Mean wet weight (g)			Mean growth rate ¹ (mg/g/day)	Reduction in growth rate (%)	Food consumption rate (mg/g/day)
				Initial	Final	Difference			
1 10/13/70	4.2	13.3	170	20.0	23.5	3.5	11.4	0	36
	10.4	13.3	170	19.6	23.0	3.4	11.4		
2 11/18/70	5.7	13.3	170	19.7	23.1	3.4	11.1	6	46
	10.3	13.9	170	19.8	23.5	3.7	11.8		
3 9/25/70	4.7	16.0	170	19.2	24.0	4.8	15.5	20	46
	9.6	16.5	170	19.2	25.2	6.0	19.4		
4 4/12/71	6.0	16.6	170	18.3	23.1	4.9	16.8	14	47
	10.0	16.8	170	18.6	24.5	6.1	19.5		
5 5/6/71	4.3	18.4	170	20.6	25.8	5.1	15.9	20	35
	9.7	19.0	170	20.6	27.1	6.6	19.7		
6 5/26/71	4.9	17.7	100	18.3	24.5	6.2	20.7	18	44
	9.4	18.5	100	19.2	27.5	8.3	25.4		
7 9/3/70	5.1	18.2	240	20.2	27.4	7.2	21.6	33	66
	9.3	19.0	240	19.9	31.6	11.7	32.4		
8 6/15/71	4.0	23.0	170	16.0	22.7	6.7	24.7	24	70
	9.0	23.6	170	15.1	24.2	9.1	32.6		
9 7/3/71	4.2	27.2	170	15.7	22.8	7.1	26.3	31	69
	8.4	27.6	170	14.9	25.5	10.6	38.0		
10 7/24/71	5.8	26.5	170	14.2	22.1	7.9	31.0	17	79
	8.3	26.8	170	14.4	24.6	10.2	37.3		

¹ Mean growth rates were calculated on the basis of the growth of individual bass. See Appendix I.

weight gain was calculated by dividing the amount of wet weight gained during the test period by the mean weight (i. e., the average of the initial and final wet weights) of the individual bass. The gain in weight per mean gram of bass was then divided by the length of the experiment in days. The growth rates of the individual bass were averaged to provide mean growth rates for each experiment.

The food consumption rates were also expressed in milligrams per mean gram of bass per day ($\text{mg}/\bar{\text{g}}/\text{day}$). They were calculated by dividing the total wet weight of mosquitofish consumed by the average total weight of bass in the pond during the test period, and finally by the number of days in the test period.

Figure 3 shows the relationship between the growth rates of largemouth bass held at high and moderately reduced oxygen concentrations at an initial prey density of 170 g/pond and temperatures ranging from 13.3 to 27.6 C. The upper curve was fitted to the growth rates of individual bass reared near the air-saturation level, and the lower curve was fitted to the growth rates of individual bass reared at oxygen levels 4 to 6 mg/liter below air-saturation levels, with the exception of the values plotted at 26.5 C. The values of 26.5 C were not used since the dissolved oxygen concentration of the pond was maintained only about 2.5 mg/liter below air saturation. Both curves were fitted by eye. As can be seen from the upper curve, the mean growth rate of the bass reared at the near the air-saturation level

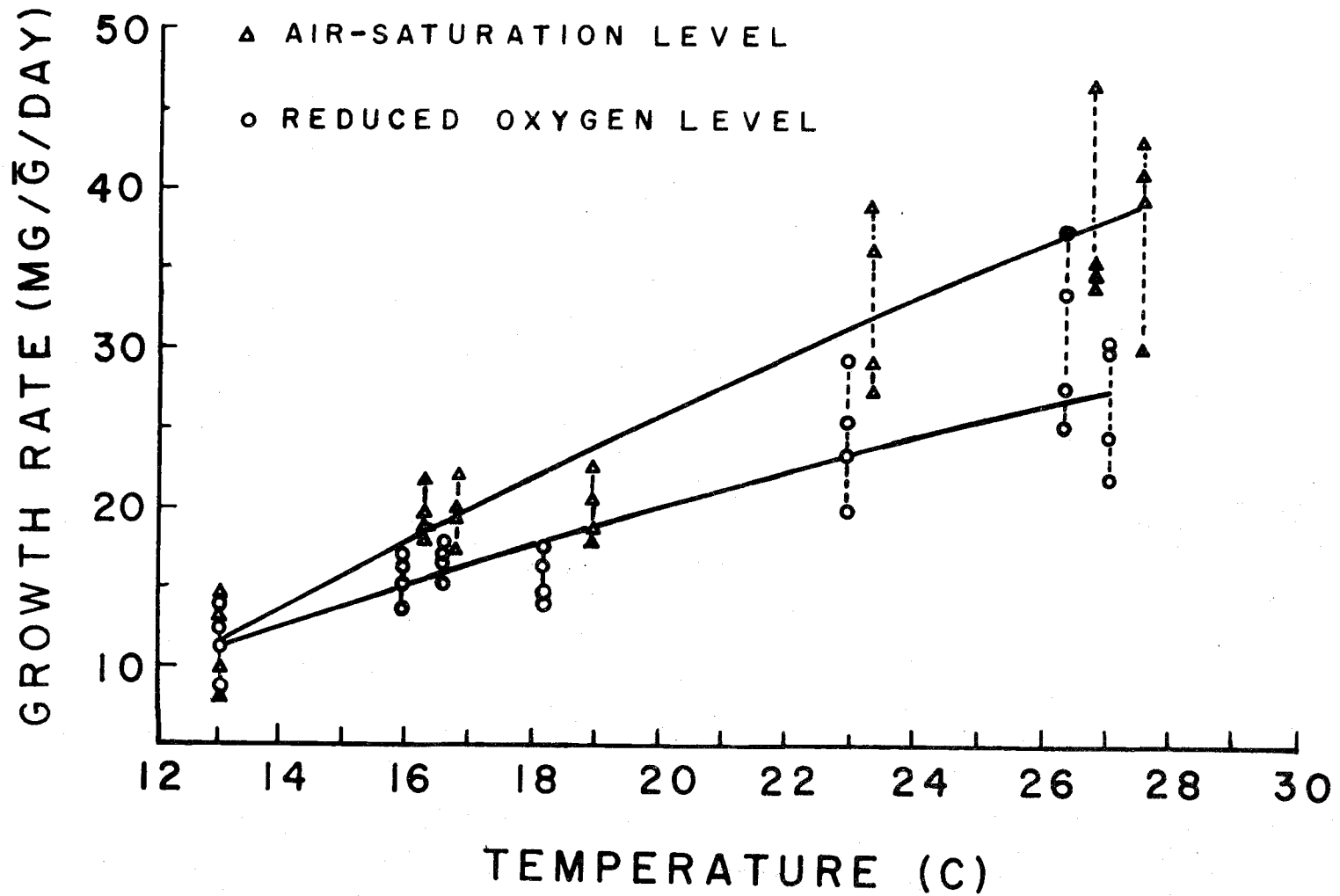


Figure 3. Relationship between the growth rates of individual largemouth bass reared in the experimental ponds at high and reduced dissolved oxygen levels, and temperatures ranging from 13.3 to 27.6 C. The ponds were stocked with an initial mosquitofish biomass of 170 g/pond.

increased from 11.4 mg/ \bar{g} /day at 13 C to 38 mg/ \bar{g} /day at 27 C. At the reduced oxygen levels a similar increase in temperature resulted in an increase in mean growth rates from 11.4 mg/ \bar{g} /day at 13 C to 27 mg/ \bar{g} /day at 27 C. The difference in the position of the two curves at temperatures above 13 C illustrates the amount of growth was depressed by a 4 to 6 mg/liter reduction in dissolved oxygen concentration at each test temperature. The greatest reduction in growth rate occurred as fish grew more rapidly at higher temperatures. The vertical distance between the points plotted at each test temperature shows that the variation between growth rates of individual bass was also greater as the bass grew more rapidly.

In experiments 5, 6, and 7, largemouth bass were exposed to initial prey densities of 170, 100 and 240 g/pond respectively. During the experiments the ponds were maintained at about 18 C and dissolved oxygen concentrations near air saturation and 4.7 mg/liter (Table 1). Bass maintained at an initial mosquitofish density of 240 g/pond grew substantially more than those maintained at either of the lower prey densities. The food consumption and growth rates of bass held at reduced dissolved oxygen levels were restricted at all three prey densities tested, but the percent reduction in growth rate was greater at higher prey densities.

An unusual relationship was observed between the growth rates of the bass reared at different densities in experiments 5 and 6. In

experiment 6, bass maintained at an initial prey density of 100 g/pond had a mean growth rate of 20.7 mg/ḡ/day at air saturation and 25.4 mg/ḡ/day at the reduced dissolved oxygen level. Even though the ponds were maintained at a slightly higher temperature and an initial prey density of 170 g/pond in experiment 5, the mean growth rates at the high and the reduced dissolved oxygen levels were only 19.7 and 15.9 mg/ḡ/day, respectively. The unexpectedly low growth rates of the bass in experiment 5, were probably due to changes in the behavior patterns of the sub-adult bass during the spring.

As the mosquitofish were preyed upon by the bass during the experiments, the total weight (density) in each pond was gradually reduced. The weights of mosquitofish stocked in the ponds at the start of each test period and that recovered when the experiment was terminated are recorded in Table 2. Since forage fish were not added during the course of the experiments, the prey densities normally fell to about 40 to 60 percent of the initial level by the end of the experiment. At a low prey density of 100 g/pond, however, the bass in experiment 6 consumed 74 percent of the mosquitofish initially added. Due to the lower food consumption rates of bass held at the reduced dissolved oxygen level in each experiment, the greatest variation in forage fish density occurred in the pond held at air-saturation level, except at low temperatures. This may have somewhat moderated the apparent effect of dissolved oxygen concentration

Table 2: Initial and final densities, and sample weights and caloric values of mosquitofish used in the pond experiments and the estimated food consumption rates of the juvenile largemouth bass.

Experiment No. and date	Prey density (g/pond)			Food consumption rate of bass (mg/g/day)	Initial sample			Final sample		
	Initial	Final	Difference		wet (g)	dry (g)	caloric (cal/g dry wt)	wet	dry	caloric (cal/g dry wt)
1 10/13/70	170	123	47	36	5.0	1.34	5746	5.02	1.31	5463
	170	127	43	36				5.07	1.34	5545
2 11/18/70	170	113	57	46	5.0	1.38	5518	5.0	1.30	5020
	170	113	57	48				5.0	1.31	5094
3 9/25/70	170	115	55	46	5.0	1.32	5594	5.0	1.34	5661
	170	106	64	51				5.0	1.36	5571
4 4/12/71	170	119	51	47	11.65	1.93	4784	10.86	1.81	4934
	170	107	63	56				11.06	1.86	4824
5 5/6/71	170	124	46	35	11.29	2.05	4921	11.06	1.97	4947
	170	106	64	48				11.15	2.00	5026
6 5/26/71	100	47	53	44	13.25	2.89	5053	11.74	2.61	5127
	100	26	74	57				12.37	2.68	5072
7 9/3/70	240	154	86	66	5.1	1.28	5206	5.0	1.18	5248
	240	117	123	85				5.2	1.36	5216
8 6/15/71	170	94	76	70	13.39	3.08	5112	10.31	2.57	5087
	170	73	97	89				11.74	2.89	5139
9 7/3/71	170	96	74	69	13.87	3.17	5167	14.15	3.53	5136
	170	69	101	96				14.26	3.57	5118
10 7/24/71	170	90	80	79	14.44	3.97	5182	15.43	4.06	5214
	170	72	98	89				16.62	4.37	5286

on growth since food became relatively more abundant in the pond maintained at lower oxygen concentration toward the end of the experiment, even though the initial prey biomass was the same in each pond.

The wet and dry weights, and caloric values of the mosquitofish samples collected before and after each experiment are presented in Table 2. An estimate of change in the condition of the mosquitofish can be made by comparing the ratio of dry to wet weights or the caloric values of the initial samples to those of the final samples. The data in Table 2 show that there was little or no change in the condition of the mosquitofish during the experiments, except in experiment 2. In the excepted experiment the mosquitofish appear to have lost weight.

The results of statistical tests computed to show experimental differences in the individual growth rates of the bass reared at high and reduced dissolved oxygen levels in each experiment are presented in Table 3. The growth rates of bass reared at high dissolved oxygen levels were statistically compared to the growth rates of those reared simultaneously at reduced levels of dissolved oxygen. At the 95 percent confidence level, the "t-test" values computed from the growth rates show a significant difference between all of the samples compared, except for those observations recorded in experiments 1, 2, and 10. Experiments 1 and 2 were conducted at a relatively low

Table 3. Statistical comparison between the growth rate values of juvenile largemouth bass reared at high and low dissolved oxygen levels in the experimental ponds. All values are based on wet weights.

Experiment number and date	Mean dissolved oxygen (mg/l)	Mean temperature (C)	Initial prey density (g/pond)	Mean growth rate ¹ (mg/g/day)	Reduction in growth rate (%)	Standard error of the mean	Variance	T ² value
1 10/13/70	4.2	13.3	170	11.3	0	1.15	5.31	0.01
	10.1	13.3	170	11.3		1.25	6.27	
2 11/18/70	5.7	13.3	170	11.1	6	0.56	1.26	0.56
	10.3	13.9	170	11.8		1.15	5.36	
3 9/25/70	4.7	16.0	170	15.5	20	0.60	1.47	3.76
	9.6	16.5	170	19.4		0.81	2.64	
4 4/12/71	6.0	16.6	170	16.8	14	0.55	1.21	2.50
	10.0	16.8	170	19.5		0.91	3.34	
5 6/6/71	4.3	18.4	170	15.9	20	0.66	1.72	3.12
	9.7	19.3	170	19.7		1.02	4.19	
6 5/26/71	4.9	17.7	100	20.7	18	1.17	5.45	3.16
	9.4	18.5	100	25.4		0.90	3.25	
7 9.25/70	5.1	18.2	240	21.6	33	0.85	2.89	4.27
	9.6	19.0	240	32.4		2.36	22.40	
8 6/15/71	4.0	23.0	170	24.4	24	1.91	14.69	2.41
	9.1	23.6	170	32.6		2.75	30.35	
9 7/3/71	4.2	27.2	170	26.3	31	1.98	15.83	3.37
	8.4	27.6	170	38.0		2.83	32.14	
10 7/24/71	5.8	26.5	170	31.0	17	2.80	31.45	1.49
	8.3	26.8	170	37.3		3.22	41.53	

¹Statistical samples consisted of the growth rate values of the 4 bass from each of the two experiment ponds.

²One-tailed T-table value at 95% confidence level with 6 degrees of freedom = 1.943.

temperature (near 13 C) and the difference in the dissolved oxygen concentrations tested had essentially no effect on the growth or food consumption of the bass. Experiment 10 was maintained at 26 C, a relatively high temperature, resulting in a large variation between the growth rate values within the samples, but the small reduction in dissolved oxygen (8.3 mg/liter to 5.8 mg/liter) caused only a small difference in growth rate values between the two samples. The variance within all of the samples increased with temperature and was usually greater at the higher oxygen level in each experiment.

Figure 4 illustrates the relationship between the mean growth rates and food consumption rates of largemouth bass held in the ponds for 2-week test periods. The growth rate and food consumption values plotted in Figure 4 were obtained from Table 1. Values are not included for experiment 2, since the mosquitofish appear to have lost substantial weight during the test period. Although several different variables are involved, the coefficient of linear correlation between the mean growth and food consumption rates of bass reared in the ponds was 0.96. This strong relationship suggests that regardless of the factors controlling food consumption, the proportion of the consumed food materials required for metabolic processes remained the same with increasing consumption rates.

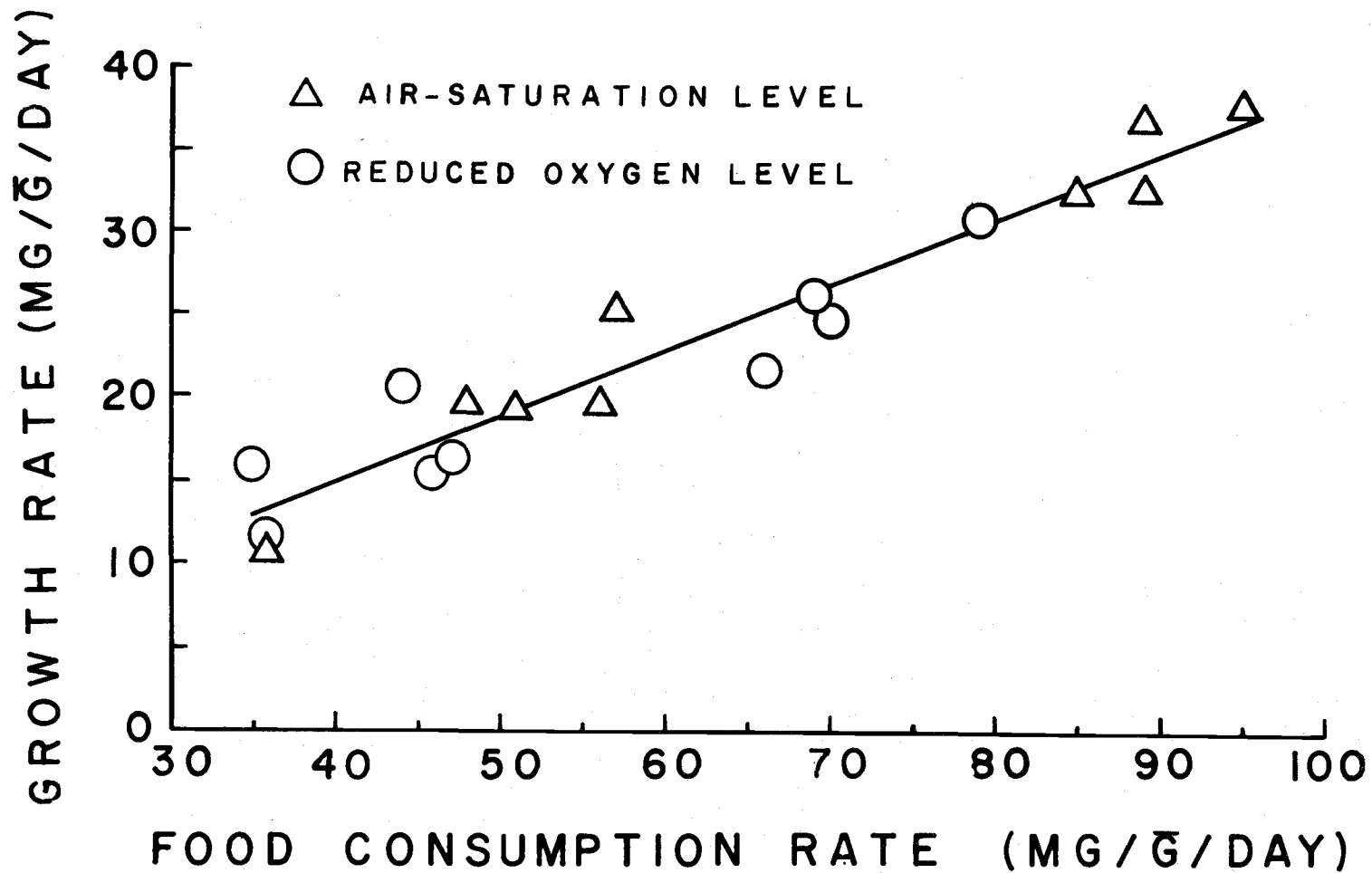


Figure 4. Mean growth rates relative to the rates of food consumption of largemouth bass reared in the experimental ponds.

DISCUSSION

The predator-prey relationship maintained in the laboratory ponds approaches natural conditions much more closely than feeding bass in small laboratory aquaria. The simple laboratory ecosystem used in this study, however, does not approximate the numerous complex interrelationships found in natural ecosystems. Due to the complex combinations of variables in nature, it is not possible to measure food consumption or metabolism, and very difficult to segregate the effects of the various factors in the environment. In the laboratory it is possible to directly measure food consumption, metabolism, and growth, and how they are effected by specific environmental factors. Understanding developed through such laboratory studies should be helpful in predicting the effect of environmental change on growth of fish in nature.

The quantity of food a fish can procure and the fate of the food after it is eaten may often be determined by environmental factors. The availability of food usually limits food consumption in nature, but other physical factors such as dissolved oxygen concentration, and temperature may also restrict the aquisition of food and the resulting growth. After fish have met the cost of body maintenance, some margin of energy must be maintained for muscular activity and internal food handling. Many factors in the environment interact to

determine the level at which food availability, oxygen, or temperature limit metabolic processes. Environmental factors determine the potential metabolic level of fish and changes in these factors can be expected to alter this level. Warren (1971) has discussed these environmental and bioenergetic relationships in detail.

Fisher (1963) fed juvenile coho salmon, Oncorhynchus kisutch, restricted and unrestricted rations of tubificid worms in laboratory aquaria held at 18 C and dissolved oxygen levels ranging from 3 to 18 mg/liter. He found that when food was not restricted, dissolved oxygen, even at the air-saturation level, limited the consumption and growth of the coho salmon. When coho salmon were fed at a rate equal to the consumption level of fish held at 3 mg/liter, food rather than dissolved oxygen became the limiting factor, and the growth rates of the young salmon were independent of dissolved oxygen concentration. The food consumption and growth rates of the coho salmon fed restricted rations were much lower than those fed to repletion at all oxygen concentrations tested above 3 mg/liter.

In a similar study, Hutchins (1971) held juvenile coho salmon in activity chambers at 15 C and oxygen concentrations ranging from 3 to 10 mg/liter. The young salmon were fed to repletion and forced to swim at a velocity of 1.3 lengths per second. The total metabolic rates of the coho salmon were reduced at the lower dissolved oxygen concentrations tested. Since muscular activity (swimming speed)

was held constant, reductions in metabolic rate due to insufficient oxygen limited energy available for food consumption and specific dynamic action (SDA), and the resulting growth.

Lee (1969) maintained juvenile largemouth bass in the experiment ponds on various densities of mosquitofish at 20 C and dissolved oxygen near the air-saturation level. The availability of forage fish in the ponds was changed by varying the density of mosquitofish and by removing the escape cover (wire-mesh cylinders) provided. A three-fold increase in prey density resulted in only about a 1/3 increase in the food consumption and growth rate of the bass. Removal of the escape cover allowed the bass to more than double their food consumption and growth rates. These observations show that the measurement of the quantity of food per unit area (density) is not always a good indication of food availability. The predator's difficulty in locating and capturing prey must be considered along with prey density when determining food availability. During my experiments the mosquitofish remained aggregated in quite limited areas of the ponds. This schooling behavior may have influenced food availability and made it easier for the bass to obtain food even when the prey density fell to low levels.

Although the food consumption and growth rates of the bass more than doubled with large increases in prey availability in Lee's pond experiments, the estimated total metabolism of the bass

appeared to remain constant at about 26 to 27 cal/kilocal bass/day, regardless of the prey density. In addition to the pond experiments, Lee (1969) fed largemouth bass live mosquitofish at different rates at various temperatures in laboratory aquaria held at the air-saturation level. He found that the total metabolic rate of bass fed unrestricted rations in aquaria held at 20 C was 27 to 28 cal/kilocal bass/day. This is very close to the total metabolic rate estimated for the bass in the ponds at the same test temperature. Lee pointed out that 26 to 28 cal/kilocal bass/day was not the maximum metabolic rate of bass, since he recorded metabolic rates of 32 cal/kilocal bass/day for bass forced to swim against a current. The metabolic rates of swimming fish was estimated by converting oxygen consumption rates into energy terms.

Hutchins (1971) varied the swimming speed of juvenile coho salmon fed unrestricted rations in the activity chambers. In these tests the dissolved oxygen concentration was maintained near the air-saturation level. He found that the total metabolic rate of the coho salmon remained constant regardless of the level of muscular activity (swimming speed). Food consumption and growth, however, decreased with increased swimming velocity. The decrease in food consumption and growth was probably due to the utilization of a greater portion of the salmon's total metabolism for muscular activity at higher swimming speeds resulting in less energy for food consumption and SDA.

Although bass foraging in the ponds and bass fed to repletion in aquaria maintained a metabolic rate near the same level, Lee (1969) found that with reductions in food availability, the metabolic rate of bass in the ponds remained constant while the metabolic rate of the bass held in aquaria was reduced as food was restricted. Since muscular activity was minimal in the laboratory aquaria, the bass probably expended most of the energy above that necessary for body maintenance for SDA. As food availability was restricted, less SDA was required and total metabolism decreased. In the ponds, however, the bass were forced to actively forage and a greater portion of their total metabolism was comprised of muscular activity to locate and capture prey. Results presented by Lee suggest that as forage fish became more available in the ponds, more food could be captured with less effort, consumption increased, and more energy was shifted from muscular activity to SDA, but the total metabolic rate still remained at a constant level, probably limited by available dissolved oxygen.

During three of the experiments reported here, the densities of mosquitofish were varied while the temperature and dissolved oxygen concentrations were maintained at about the same levels. At reduced oxygen levels the food consumption and growth rates of the bass were substantially less at all three prey densities tested. The portion of food utilized for total metabolism by the bass during

each test period can be estimated by multiplying the consumption rate by the assimilation efficiency (estimated about 80 percent), and subtracting the growth rate. In experiment 6 the bass reared at a dissolved oxygen concentration of 9 mg/liter utilized food for metabolic processes at a rate near 20 mg/ḡ/day while the metabolic costs of fish reared at 5 mg/liter utilized food at a rate of only about 15 mg/ḡ/day, a 25 percent reduction in total metabolic rate. By following the same line of reasoning, the data in this study indicate that the total metabolic rates of the bass were a function of oxygen concentration in every case where food consumption and growth rates were reduced at lower oxygen concentrations. Since the metabolic rate of bass in the ponds was probably limited by dissolved oxygen at air saturation, a reduction in dissolved oxygen concentration restricted the metabolic rate of the bass and resulted in a reduction in food consumption and growth.

Brocksen, Davis, and Warren (1968), reported that the respiration rates of sculpin, Cottus perplexus, and cutthroat trout, Salmo clarki, foraging in laboratory streams appeared to increase with increasing food density. Respiration as defined by Brocksen et al. is the same as the term total metabolism used here. These results are contrary to those obtained with bass in the ponds. It was reported that the trout living in the streams fed mainly on organisms drifting in the current, while the sculpin fed on benthos organisms among the rocks and debris on the bottom of the streams.

These types of feeding behavior probably required a rather small, almost constant expenditure of energy for muscular activity. Since food in the laboratory streams was very limited and was probably procured more passively than in the ponds, consumption and growth was restricted by food availability. Foraging activity probably did not measurably increase as food became more sparse. In the laboratory streams, just as in laboratory aquaria where fish were maintained on restricted rations, food rather than dissolved oxygen was the factor limiting metabolism

Hutchins (unpublished data) reared juvenile coho salmon in laboratory streams similar to those used by Brocksen et al. (1968), but held at dissolved oxygen concentrations of about air-saturation, 5, and 3 mg/liter. He found that when food availability restricted food consumption to a low level (below 30 mg/g/day) the food consumption and growth rates of juvenile coho salmon feeding on drifting organisms were not restricted by the reduction of dissolved oxygen to 3 mg/liter. As the availability of food increased, however, food consumption and growth also increased, but was restricted at the reduced dissolved oxygen levels tested. The results of the studies by Hutchins and Brocksen et al. indicate that food consumption determines the rate of fish metabolism at low levels of food availability. This is certainly true when fish are not required to expend much additional energy to locate and capture food. Increased food availability resulting in higher food consumption rates, probably

increase SDA until the metabolic rates of the fish become limited by the dissolved oxygen concentration in their environment.

In the laboratory study reported by Lee (1969), the food consumption and growth rates of juvenile largemouth bass fed to repletion in aquaria increased with temperature from a low of near 33 mg/g/day consumption and 10 mg/g/day growth at 10 C to 214 mg/g/day consumption and 103 mg/g/day growth at 31 C. Lee found that although the bass consumed less at the temperatures tested when food was restricted, food consumption and growth was still a function of temperature. Brown (1957) points out that because temperature alters the rates of metabolic processes, it can be expected to have considerable effect on food consumption and growth. Since metabolic processes increase with temperature, it is reasonable to assume that the reduction of dissolved oxygen concentration would have the greatest effect on total metabolism as fish become more active at higher temperatures.

In a series of laboratory experiments using largemouth bass maintained in aquaria at 26 C on unrestricted rations of small earthworms, Stewart et al. (1967) found that growth rates of bass subjected to dissolved oxygen concentrations of 5, 4, 3, and 2 mg/liter were reduced 8.5%, 16.5%, 30% and 52%, respectively when compared to those of the bass reared at the air-saturation level. In later studies, Trent (1971) fed juvenile largemouth bass unrestricted rations of

salmonid fry in aquaria held at 20, 15, and 10 C and dissolved oxygen concentrations ranging from 2.4 to 9 mg/liter. At 20 C his data show reductions in growth similar to those reported by Stewart et al. (1967) for bass reared at 26 C. At 15 and 10 C the growth rates of bass were almost equal at all dissolved oxygen concentrations tested, except for a slight reduction in growth at 2.4 mg/liter at both temperatures.

During the study reported here, direct observations revealed that bass in the ponds were more active at higher temperatures, and the data show that they consumed and utilized more food as the temperature increased. The food consumption and growth of bass were restricted the most at the highest temperature tested (32% at 27 C), but were significantly lower at reduced oxygen levels at all temperatures tested, except at 13 C. Exposure to low temperatures probably slow metabolic processes of fish to such an extent that their total metabolic rates are not limited by oxygen except at very low concentrations. As temperatures increase, however, metabolic rates of fish increase, and even slight reductions in dissolved oxygen concentration below the air-saturation level have a marked effect on the ability of fish to feed and grow. At the relatively high temperature of 26 C, a 2.5 mg/liter reduction in oxygen concentration resulted in a 17% reduction of the mean growth rate of juvenile bass held in the ponds.

The metabolic rate of the actively feeding bass in the ponds was probably controlled by temperature and limited by dissolved oxygen concentration, except at low temperatures where the dissolved oxygen concentration had little effect. Whether the metabolic rate of fish was restricted by low food availability, temperature, or reduced dissolved oxygen concentration, the most evident effect of the lower metabolic rate was reduced food consumption and resulting growth.

Due to changes in the availability and quality of food; size, condition and behavior of fish; interspecific and intraspecific competition; and many other factors, accurate estimates of the metabolic rates of fish in nature are difficult at best. In most cases, only growth (elaboration of tissue) can be accurately measured in nature. Laboratory studies are normally not designed to approach the diversity or complexity of nature, but rather to provide simple, controlled circumstances in which the effect of environmental change can be directly measured by its effect on some life process of the fish. Laboratory studies are valuable in helping understand fish production in nature only if there is enough evidence to allow us to assume that fish react bioenergetically in a similar way, under similar environmental conditions, both in the laboratory and in nature.

Although the data are limited there is a good correlation between the effect of the reduction of dissolved oxygen at various temperatures on the growth of bass foraging in ponds and those fed to repletion in laboratory aquaria. Trent (1971) found that in laboratory aquaria held at 20 C the mean growth rate of the bass was reduced about 20% (31 mg/g/day to 25 mg/g/day) when the oxygen concentration was reduced from 9.4 to 4.4 mg/liter. In my study bass reared at 19 C and dissolved oxygen concentrations of 9.5 and 4.3 mg/liter grew 19 and 15.5 mg/g/day, respectively. This is also about a 20% reduction in growth. At 13 C the reduction of the dissolved oxygen concentration had little or no effect on the growth of largemouth bass in the ponds. Trent also reported that growth of bass was not affected by the reduction of dissolved oxygen at low temperatures (15 and 10 C) in laboratory aquaria, except for a slight reduction observed below 2.4 mg/liter. It appears, then, that at similar temperatures, reductions in the dissolved oxygen concentration restricted the growth of bass in a similar manner in both the ponds and aquaria, even though the energy budget of the bass in each case was probably different.

A linear relationship was observed between the food consumption and growth rates of the bass over the range of environmental factors tested in the experimental ponds. Pond data reported by Lee (1969) shows a similar relationship between food consumption and

growth, although the line is to the right of that obtained in my study. Lee used somewhat smaller bass, which may explain the lower position of the line. For the relationship between growth and consumption to be linear, the ratio between growth and other energy expenditures (i. e., waste, specific dynamic action, activity, and standard metabolism) must remain constant (Warren, 1971). As total metabolism increased, or food became easier to procure, the bass consumed more; but, the energy and materials utilized or lost as activity, SDA, wastes, or body maintenance increased proportionally.

The relationship between food consumption and growth indicates that when bass of nearly the same size grow at a given rate, for whatever the reason, their food consumption rate can be quite accurately predicted. This linear relationship probably would only exist over moderate ranges of environmental stress, but these ranges include conditions fish normally encounter in nature. In nature, size differences, variations in behavior, or other factors which change the relationship between the food consumption and growth of bass would limit the predictive value of this linear relationship. With the limited data in my study, therefore, it is difficult to predict what ecological significance this linear relationship may have.

Although my pond studies and other studies conducted in the laboratory have given some feeling for what effect reduced dissolved

oxygen levels will have on bass growing under natural conditions, there are many phenomena in nature which have not been considered in the laboratory yet that may alter the apparent effect of environmental change. In the studies reported here, food consumption and growth rates recorded in one experiment were significantly effected by a change in the behavior of the bass. During the experiments conducted in May of 1971, it was visually observed that the juvenile bass were very aggressive and appeared to defend certain areas of the pond against intrusion by other bass. The bass appeared to feed less often, and foraged individually rather than in groups as was the case in the other experiments. Because of this unusual behavior pattern, the bass consumed less food and grew at a slower rate during the experiment. The same behavior pattern was observed for the first 4 days of the next experiment, after which the bass became less aggressive and again fed as a group. Many such behavioral changes of fish in nature could effect the validity of assumptions made about the relationship between dissolved oxygen concentration and growth of fish in nature, if the assumptions are based on relationships which have been observed only in the laboratory.

Considering the information obtained from the studies conducted in experimental ponds and laboratory aquaria, I feel that environmental factors largely control and limit metabolic processes of similar sized bass in the same way in nature and in the laboratory.

The problem with making generalizations from food consumption and growth of fish in the laboratory to food consumption and growth of fish in nature is that the life pattern of fish in nature may demand a substantially different energy budget than the energy budget required of a fish to consume food and grow in the laboratory, even under similar environmental conditions. Although the total metabolic rate may be the same, differences in environmental stresses and behavior of fish in nature and in the laboratory may result in widely different amounts of consumption and growth at the same food availability and similar environmental conditions. Since metabolism cannot be measured in nature, changes in growth rather than changes in metabolic rate must be used as an index for the effect of environmental change. Further laboratory studies investigating how size variation, competition, behavior changes, and other natural phenomena affect the relationship between dissolved oxygen concentration and growth are needed. These studies are necessary before it can be shown that laboratory data have any real, practical and ecological significance in predicting the effect of changes in dissolved oxygen concentration on the production of fisheries in nature.

LITERATURE CITED

- American Public Health Association, American Water Works Association, and Federation of Sewage and Industrial Wastes Association, 1965. Standard methods for the examination of water, sewage, and industrial wastes. 12th ed. New York, 769 pp.
- Brocksen, R. W., G. E. Davis, and C. E. Warren. 1968. Competition, food consumption and production of sculpins and trout in laboratory stream communities. *Journal of Wildlife Management* 32:51-57.
- Brown, M. E. 1946. The growth of brown trout (*Salmo trutta* Linn.) III. The effect of temperature on the growth of two-year-old trout. *Journal of Experimental Biology* 22:145-150.
- Brown, M. E. (Editor). 1957. *The Physiology of Fishes*. Vol. 1, Metabolism. Academic Press Inc., New York, xiii + 445 pp.
- Doudoroff, P., and D. L. Shumway. 1970. Dissolved Oxygen Requirements of Freshwater Fishes. European Inland Fisheries Advisory Commission, Food and Agricultural Organization of the United Nations, Rome, 291 pp.
- Doudoroff, P., and C. E. Warren. 1965. Dissolved oxygen requirements of fishes. In: *Biological problems in water pollution* (Transaction 1962 Seminar). United States Public Health Service Publication 999-WP-25, 145-155.
- Ellis, M. M. 1937. Detection and measurement of stream pollution. *Bulletin of the United States Bureau of Fisheries* 48(22):365-437.
- Fisher, R. J. 1963. Influence of oxygen concentration and of its diurnal fluctuations on the growth of juvenile coho salmon. M.S. thesis. Oregon State University, Corvallis, 48 pp.
- Fry, F. E. J. 1960. The oxygen requirements of fish. In: *Biological Problems in water pollution*. Technical Report W60-3, Robert A. Taft Sanitary Engineering Center, United States Public Health Service, pp. 106-109.

- Gibbs, M. 1970. The inhibition of Photosynthesis by Oxygen, *American Scientist* 58:634-640.
- Groves, A. B., and A. J. Novotny. 1965. A thermal-marking technique for juvenile salmonids. *Transactions of the American Fisheries Society* 94:386-389.
- Herrmann, R. B., C. E. Warren, and P. Doudoroff. 1962. Influence of oxygen concentration of the growth of juvenile coho salmon. *Transactions of the American Fisheries Society*, 91:155-167.
- Hutchins, F. E. 1971. Influence of dissolved oxygen and swimming velocity on the food consumption and growth of juvenile coho salmon. Manuscript, M. S. thesis in preparation, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.
- Jones, J. R. E. 1964. *Fish and river pollution*. Butterworth, Inc., Washington, 203 pp.
- Lee, R. A. 1969. Bioenergetics of feeding and growth of largemouth bass in aquaria and ponds. M. S. thesis. Oregon State University, Corvallis, 63 pp.
- Mount, D. I. 1964. Additional information on a system for controlling the dissolved oxygen content of water. *Transactions of the American Fisheries Society* 93:100-103.
- Stewart, N. E., D. L. Shumway, and P. Doudoroff. 1967. Influence of oxygen concentration on the growth of juvenile largemouth bass. *Journal of the Fisheries Research Board of Canada* 24:334-335.
- Swift, D. R. 1955. Seasonal variation in the growth rate, thyroid gland activity and food reserves of brown trout (Salmon trutta Linn.) *Journal of Experimental Biology* 32:751-764.
- Trent, T. W. 1971. The influence of temperature and oxygen concentration on the food consumption and growth of largemouth bass and coho salmon. Manuscript, M. S. thesis in preparation, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.
- Warren, C. E. 1971. *Biology and Water Pollution Control*, W. B. Saunders Company, Philadelphia, 424 pp.

APPENDIX

Appendix 1. Mean and range of temperature and dissolved oxygen concentration, and lengths, weights, growth rates, and caloric values of large-mouth bass used in the pond experiments.

Experiment No. and date	Mean temperature and range (C)	Mean dissolved oxygen and range (mg/liter)	Total length (cm)		Wet weight (g)			Growth rate (mg/ḡ/day)	Final dry weight (g)	Final caloric value (cal/g)	
			Initial	Final	Initial	Final	Difference				
1 10/13/70	13.3 (11.5-14.7)	4.2 (3.7-5.4)	11.9	12.4	20.7	24.0	3.3	10.5	6.56	5210	
			11.9	12.4	20.1	22.7	2.7	8.6	6.09	5166	
			11.7	12.3	19.7	23.9	4.2	13.9	6.52	5565	
			11.6	12.2	19.6	23.3	3.7	12.3	6.40	5257	
	13.3 (11.6-15.6)	10.4 (10.2-10.9)	11.7	12.1	19.7	23.5	3.9	12.8	6.52	5436	
			11.8	12.2	19.9	24.2	4.3	13.9	6.53	5450	
			11.7	12.1	19.4	22.0	2.6	8.5	6.18	5234	
			11.6	12.2	19.2	22.1	2.9	9.9	5.96	5115	
	2 11/18/70	13.3 (11.7-15.5)	4.2 (3.8-5.7)	11.8	12.2	20.3	23.6	3.3	10.7	6.54	5556
				11.6	11.9	19.6	23.4	3.8	12.7	6.46	5598
				11.6	12.1	19.2	22.4	3.2	11.1	6.15	5237
				11.7	12.3	19.9	22.8	3.0	10.0	6.25	5428
13.9 (12.8-16.1)		10.3 (10.1-10.8)	11.5	11.8	18.4	20.8	2.4	8.9	5.76	5561	
			11.8	12.1	19.9	24.0	4.1	13.4	6.52	5481	
			11.8	12.3	20.7	24.2	3.5	11.1	6.67	5580	
			11.7	11.9	20.3	24.7	4.4	13.9	6.87	5569	
3 9/25/70	16.0 (13.8-17.2)	4.7 (3.7-5.6)	11.8	12.6	20.3	25.1	5.0	15.6	6.83	5354	
			11.6	12.4	19.1	24.1	5.0	16.4	6.44	5115	
			11.4	12.6	17.4	21.9	4.5	16.3	5.84	5322	
			11.6	12.5	20.3	24.7	4.3	13.7	6.77	5192	
	16.6 (13.2-19.6)	9.6 (9.4-10.4)	11.8	12.5	18.2	24.7	6.4	21.4	6.72	5350	
			11.7	12.7	19.4	25.6	6.3	19.9	6.81	5250	
			11.5	12.2	18.9	24.5	5.6	18.5	6.49	5191	
			11.7	12.8	20.4	26.2	5.8	17.7	7.07	5366	

Appendix 1. Continued.

Experiment No. and date	Mean temperature and range (C)	Mean dissolved oxygen and range (mg/liter)	Total length (cm)		Wet weight (g)			Growth rate (mg/ḡ/day)	Final dry weight (g)	Final caloric value (cal/g)
			Initial	Final	Initial	Final	Difference			
4 4/12/71	16.6 (15.2-19.1)	6.0 (5.2-7.1)	11.5	12.1	18.3	22.6	4.3	15.2	5.97	5147
			11.5	12.3	18.2	23.3	5.1	17.4	6.00	5024
			11.6	12.2	18.6	23.8	5.2	17.5	6.05	5049
			11.6	12.3	18.1	23.0	5.0	17.2	5.87	
	16.8 (14.3-20.7)	9.6 (9.3-10.2)	11.6	12.6	18.9	24.7	5.7	19.2	6.25	4892
			11.5	12.2	18.4	23.5	5.1	17.4	5.94	5070
			11.7	12.4	18.8	25.6	6.8	21.8	6.19	4856
			11.7	12.5	18.3	24.1	5.8	19.6	6.14	5066
5 5/6/71	18.4 (16.2-19.6)	4.3 (2.4-4.8)	12.7	12.9	21.3	26.2	4.9	14.8	6.52	4839
			12.2	12.7	19.7	24.8	5.1	16.3	6.15	4872
			12.2	12.5	21.5	26.5	5.0	14.9	7.19	4937
			12.2	12.7	20.0	25.6	5.1	17.5	6.33	4847
	19.0 (16.0-20.2)	9.7 (9.1-10.0)	12.3	12.8	20.7	27.6	6.9	20.3	7.33	5118
			12.3	12.8	20.3	26.2	5.9	18.2	6.33	5109
			12.1	12.9	19.6	26.8	7.2	22.3	7.80	4912
			12.5	12.9	21.7	27.9	6.2	17.8	7.37	5276
6 5/26/71	17.7 (16.2-18.4)	4.9 (3.2-5.2)	11.7	12.1	17.9	22.9	5.0	17.6	5.66	4806
			11.9	12.6	19.0	25.9	6.9	22.0	6.46	4763
			11.8	12.5	19.0	25.4	6.4	20.5	6.48	4952
			11.6	12.2	17.3	23.9	6.6	22.9	5.99	4955
	18.5 (15.9-19.2)	9.4 (9.2-9.8)	12.1	12.9	20.1	28.8	8.7	25.3	6.10	4963
			11.9	12.6	19.6	27.9	8.3	25.0	6.98	4887
			11.8	12.6	19.8	29.4	9.6	27.9	7.38	5027
			11.6	12.3	17.1	23.9	6.8	23.5	5.28	4961

Appendix 1. Continued.

Experiment No. and date	Mean temperature and range (C)	Mean dissolved oxygen and range (mg/liter)	Total length (cm)		Wet weight (g)			Growth rate (mg/g ² /day)	Final dry weight (g)	Final caloric value (cal/g)
			Initial	Final	Initial	Final	Difference			
7 9/3/70	18.2 (15.4-20.2)	5.1 (4.2-6.2)	11.4	12.7	20.3	27.6	7.3	21.7	7.43	5170
			11.5	12.8	20.7	28.5	7.8	22.7	7.72	5270
			11.5	12.4	19.3	26.7	7.4	22.9	7.13	5244
			11.6	12.5	20.5	26.9	6.4	19.2	6.90	5081
	19.0 (15.4-21.8)	9.3 (8.9-10.1)	11.9	13.5	21.2	33.3	12.2	32.0	9.23	5361
			11.7	13.3	18.8	32.5	13.7	38.2	9.83	5338
			11.4	13.0	18.6	29.7	11.1	32.7	8.10	5112
			11.4	13.2	21.0	30.6	9.6	26.6	8.58	5279
8 6/15/71	23.0 (18.3-25.5)	4.0 (3.0-4.6)	11.4	12.1	16.6	22.0	5.4	19.8	5.60	--
			11.2	12.0	15.1	22.8	7.7	29.1	5.71	--
			11.3	12.2	16.1	22.7	6.6	23.6	5.63	--
			11.4	12.2	16.3	23.3	7.0	25.3	5.78	--
	23.6 (19.4-25.8)	9.0 (8.5-9.3)	11.2	12.6	16.0	26.7	10.8	36.0	6.87	--
			11.1	12.0	14.4	21.7	7.6	28.9	5.42	--
			11.2	12.1	15.1	22.1	7.0	26.9	5.52	--
			11.1	12.3	15.1	26.2	11.1	38.6	6.55	--
9 7/3/71	27.2 (21.4-30.1)	4.2 (3.2-4.7)	11.2	11.9	15.4	20.9	5.5	21.6	5.62	4812
			11.2	11.9	16.3	23.1	6.7	24.4	6.06	4935
			11.2	12.4	15.3	23.3	8.0	29.4	6.00	4887
			11.1	12.2	15.7	24.0	8.2	29.8	6.10	5027
	27.6 (20.7-31.4)	8.4 (7.4-9.1)	10.8	12.5	14.2	25.3	11.1	40.2	6.66	5006
			11.0	12.1	15.2	23.2	8.0	29.8	6.01	4987
			10.9	12.6	14.6	25.6	11.0	39.1	6.81	5159
			11.0	12.9	15.5	28.8	13.3	42.8	7.60	5162

Appendix 1. Continued.

Experiment No. and date	Mean temperature and range (C)	Mean dissolved oxygen and range (mg/liter)	Total length (cm)		Wet weight (g)			Growth rate (mg/g/day)	Final dry weight (g)	Final caloric value (cal/g)
			Initial	Final	Initial	Final	Difference			
10 7/24/71	26.5 (22.0-31.6)	5.8 (4.0-6.6)	10.8	11.8	13.7	20.3	6.6	27.6	5.03	--
			10.9	12.1	14.9	24.0	9.1	33.3	5.81	--
			10.7	11.7	14.0	20.0	6.0	25.2	4.86	--
			10.8	12.6	14.1	24.2	10.1	37.7	5.91	--
	26.8 (21.3-32.7)	8.3 (7.8-9.2)	11.0	12.5	15.6	25.6	10.0	34.9	6.58	--
			11.0	12.5	13.8	22.7	8.8	34.5	5.81	--
			10.8	12.4	14.2	22.8	8.6	33.2	6.04	--
			11.1	13.1	13.8	27.4	13.6	47.0	7.36	--