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Dean L. Shumway

A study was conducted at the Oak Creek Laboratory of the Pacific Cooperative Water Pollution Laboratories, Oregon State University, to determine the influence of temperature, season of the year, and food availability on the food consumption and growth of largemouth bass, (*Micropterus salmoides*). The experiments were performed during 1966 and 1967.

The relationships between food consumption and growth of largemouth bass held in aquaria at 20 C during summer, fall, winter, and spring were essentially the same, suggesting that season of the year has little to do with this relationship. Variations of test temperature, however, were found to alter materially this relationship. Within the range of water temperatures tested (10 to 31 C), the food consumption and growth rates of largemouth bass fed to excess on mosquitofish (*Gambusia affinis*) increased with temperature. The maintenance ration and the rate of weight loss

when the bass were not fed also increased with temperature.

Food consumption and growth rates were determined for largemouth bass held in specially constructed experimental ponds for 10-day periods during the summer at about 21 C and confronted with widely varying densities of mosquitofish. The food consumption and growth rates of largemouth bass increased with increase of prey density, nearly reaching a plateau at the highest density provided. The estimated energetic cost of activity of largemouth bass appeared to decrease with increased prey density, whereas the estimated energetic cost of specific dynamic action appeared to increase. However, the total metabolic rate of largemouth bass remained nearly constant at about 26-27 cal/kilocalorie of bass/day.

Bioenergetics of Feeding and Growth of Largemouth Bass in Aquaria and Ponds

by

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INTRODUCTION

Freshwater fish may be exposed to widely ranging food densities and temperatures in nature. Food consumption and growth rates of fish are known to vary from one set of ecological conditions to another and are influenced by changes in food availability, season, and temperature. The effects of prey density, season, and temperature on rates of food consumption and growth of fish thus are important considerations in the study of fish production.

Very few studies have developed relationships between food availability, rates of food consumption, and rates of growth of fish. Ivlev (1961) used a mathematical model to relate food density, food consumption, and growth of a plankton-eating fish (Alburnus alburnus) in a hatchery pond. Maximum rations and routine and active metabolism rates of fish were determined in the laboratory. Numerous assumptions had to be made in developing the model, since growth rate of the fish in the pond was determined at one level of food availability only.

More recently, work has been reported on the effects of prey density on food consumption, growth, assimilation, and respiration of sculpins (Cottus perplexus) and cutthroat trout (Salmo clarki clarki) in laboratory streams by Brocksen et al. (1968). They, however, estimated food consumption rates from growth rates of the fish by comparing these growth rates with those of fish held in aquaria on varying known food rations. Their approach involves the assumption that the activity and gross food conversion efficiency of fish held in aquaria did not differ materially from those of the fish in the laboratory streams.

There is much literature pertaining to the effect of temperature on food consumption and growth of fish, but many questions relating to this problem remain unanswered. Anderson (1959) has reported that both temperature and season influenced the food consumption and growth of individual bluegills (Lepomis macrochirus Rafinesque) when held in laboratory aquaria and in live-box feeding cages placed in a Michigan lake. An understanding of the effects of temperature and season on bass growth was necessary to facilitate understanding of bass growth data obtained in the pond experiments reported here, in which temperature was not controlled.

The main objective of this study was to determine through direct measurements of both food consumption and growth the effect that changing prey density would have on the food consumption and growth rates of largemouth bass (Micropterus salmoides) in a pond environment. Information was obtained also on the effect of temperature and season on food consumption and growth of largemouth bass held in laboratory aquaria.

During the summer of 1967, juvenile largemouth bass were held in experimental ponds for 10-day periods and confronted with widely varying densities of mosquitofish (*Gambusia affinis*) in order to obtain information on the bioenergetics of a predator-prey relationship. A bioenergetic representation of how fish utilize a food resource, as proposed by Warren and Davis (1967), was used as a model in this study. Since it is difficult to relate what happens in nature to what occurs in the laboratory, experiments were conducted in experimental ponds, thus approaching natural conditions.

In conjunction with the experimental pond study, a series of laboratory experiments were conducted to determine the effect of temperature and season on the relationship between food consumption and growth of juvenile and adult largemouth bass held at nearly constant temperatures in laboratory aquaria. In these experiments, growth rates of bass were measured at various food consumption rates over a range of temperatures for each season of the year.

When predator-prey relationships have been determined under somewhat controlled conditions, more complex relationships present in a natural environment may be less difficult to understand. The results reported in this paper are to serve as a foundation for future studies of predator-prey relationships in experimental ponds at various dissolved oxygen concentrations. The present study was undertaken because more research is needed to determine the effect, if any, that reduced oxygen concentrations have on fish under conditions more natural than those found in the laboratory. This study is, therefore, one segment of a comprehensive investigation of the dissolved oxygen requirements of fish.

EXPERIMENTAL APPARATUS, METHODS AND MATERIALS

Experimental Animals

The largemouth bass used in these experiments were collected from three small ponds located in the Willamette Valley of Oregon. It was necessary to use bass from different sources, as sufficient numbers of bass of the desired size could not be obtained from a single location. Once seined, the bass were quickly transported to the Oak Creek Laboratory, where they were placed in an outdoor pond or in a 50-gal (190-liter) glass aquarium located in a 20 C constant-temperature room. Bass which were placed in the outdoor pond were exposed to varying water temperatures, whereas those placed in the 50-gal glass aquarium were held at a water temperature of approximately 20 C.

The mosquitofish used as food for the bass were collected from Oregon State University's Soap Creek ponds, transported to the Oak Creek Laboratory, and held outdoors in a wooden tank or in a 50-gal glass aquarium located in a 20 C constant-temperature room. Mosquitofish that were deformed, unhealthy in appearance, in advanced stages of pregnancy, excessively large, or very small were not used as food in these experiments. The mosquitofish were fed a commercial guppy food until their use in experiments.

Experimental Apparatus

Laboratory Apparatus

The laboratory apparatus used in this study was designed to provide a flow of water of controlled temperature to four test vessels (20-gal glass aquaria) containing the test fish. An opaque, plastic aquarium divider with numerous small, round perforations usually was used to divide each test vessel into two test chambers, each 31 cm wide by 31 cm long by 31 cm deep. In experiments 4 and 5, the plastic dividers were not utilized, and each vessel became a single, large test chamber. The apparatus was located in constant-temperature rooms continuously illuminated with either fluorescent or incandescent lights. Figure 1 is a schematic drawing of the laboratory apparatus used in this study, with only one of the four test vessels shown. The sides of each test vessel were wrapped with black plastic sheeting to reduce the effect on the experimental fish of outside disturbances by people working in the area.

Filtered water supplied from a small spring-fed stream was introduced into a constant-head box, where it was heated to the desired temperature by a thermostatically controlled, stainless-steel immersion heater and vigorously aerated with compressed air. The warmed water then flowed through plastic tygon tubing and a flow-adjustment stopcock, into the test vessel at a rate of 100 to 300

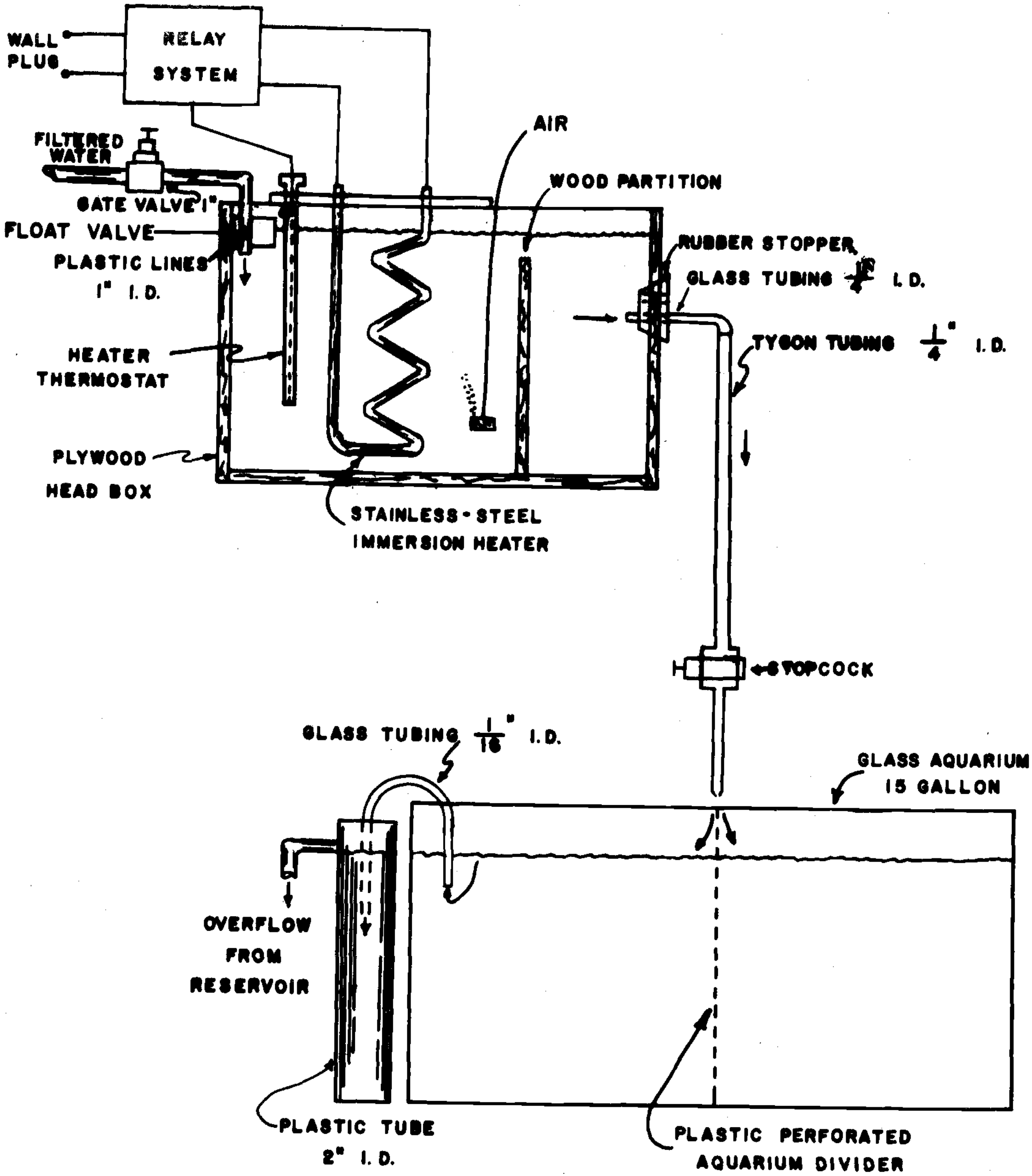

Figure 1. Schematic drawing of the laboratory apparatus.

ml/min. The dissolved oxygen concentration of the water in each test chamber was maintained at near the air-saturation level by bubbling air through the water in each chamber. The desired water level was maintained in each test vessel by connecting the vessel with a siphon to a small constant-head reservoir attached to the outside of the vessel.

Pond Apparatus

Two oval, concrete experimental ponds, each with an underwater observation chamber, were designed and constructed for this study (Fig. 2). Each pond is approximately 7.3 m long, 6.1 m wide, and 1 m deep and will hold 5,000 gal (19,000 liters) of water. The ponds were designed to provide a band of shallow area, approximately 0.5 m wide, around the periphery of each pond. From the shallow area around the periphery, the contours of the pond slope sharply to the bottom. The wooden rectangular observation chamber is 3.7 m long, 1.3 m wide, 1.8 m high, and projects 3 m into the middle of each pond. Each chamber was fitted with seven 46-by-76 cm underwater observation ports; three ports are on each side of the chamber and one is at the end. The observation chambers and cracks in the concrete which occurred after construction of the ponds were covered with fiberglass to prevent leakage of water from the pond and to protect the wooden chambers from deterioration.

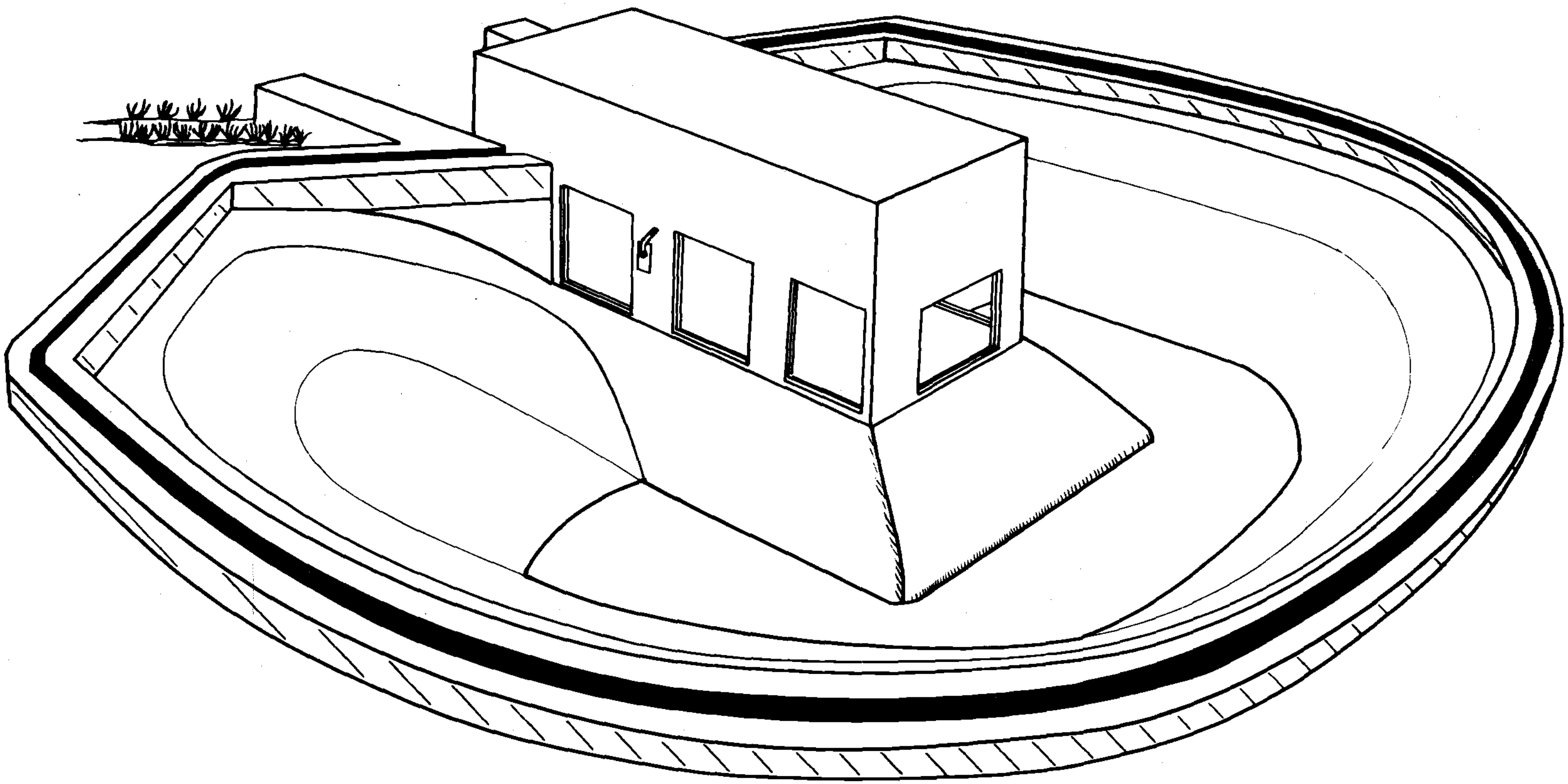

Figure 2. Schematic drawing of one of the two experimental ponds used in this study. Each pond was equipped with an observation chamber and an adjustable standpipe to maintain the desired water level in the pond. Each pond is approximately 7.3 m long, 6.1 m wide, and 1 m deep and will hold about 5,000 gallons (19,000 liters) of water.

Galvanized chicken wire, with a mesh size of about 2.5 cm, was rolled into cylinders 100 cm long and 15 cm in diameter and painted with a nontoxic paint. These rolls of wire were linked end to end and placed in the shallow area around the periphery of the pond (Fig. 3). Well water was introduced into each pond at a rate of 4 to 8 liters/min.

Experimental Methods

Aquaria Experiments

Fourteen to sixteen days before the start of an experiment, bass of nearly uniform size were selected from the available stock and placed in the experimental apparatus. One fish was placed in each test chamber, with the exception of two chambers which received two fish each. The water temperature in the apparatus was then adjusted to the desired level. During this acclimation period, the bass were fed to repletion on mosquitofish every other day. The bass were not fed for 48 to 56 hr prior to the start of each experiment. This was done to allow the elimination of food and fecal material from their digestive tract before weighing.

At the start of each experiment, the acclimated bass were removed from the apparatus, and lightly anesthetized with MS 222 (tricaine methanesulfonate). Each was weighted and measured, and

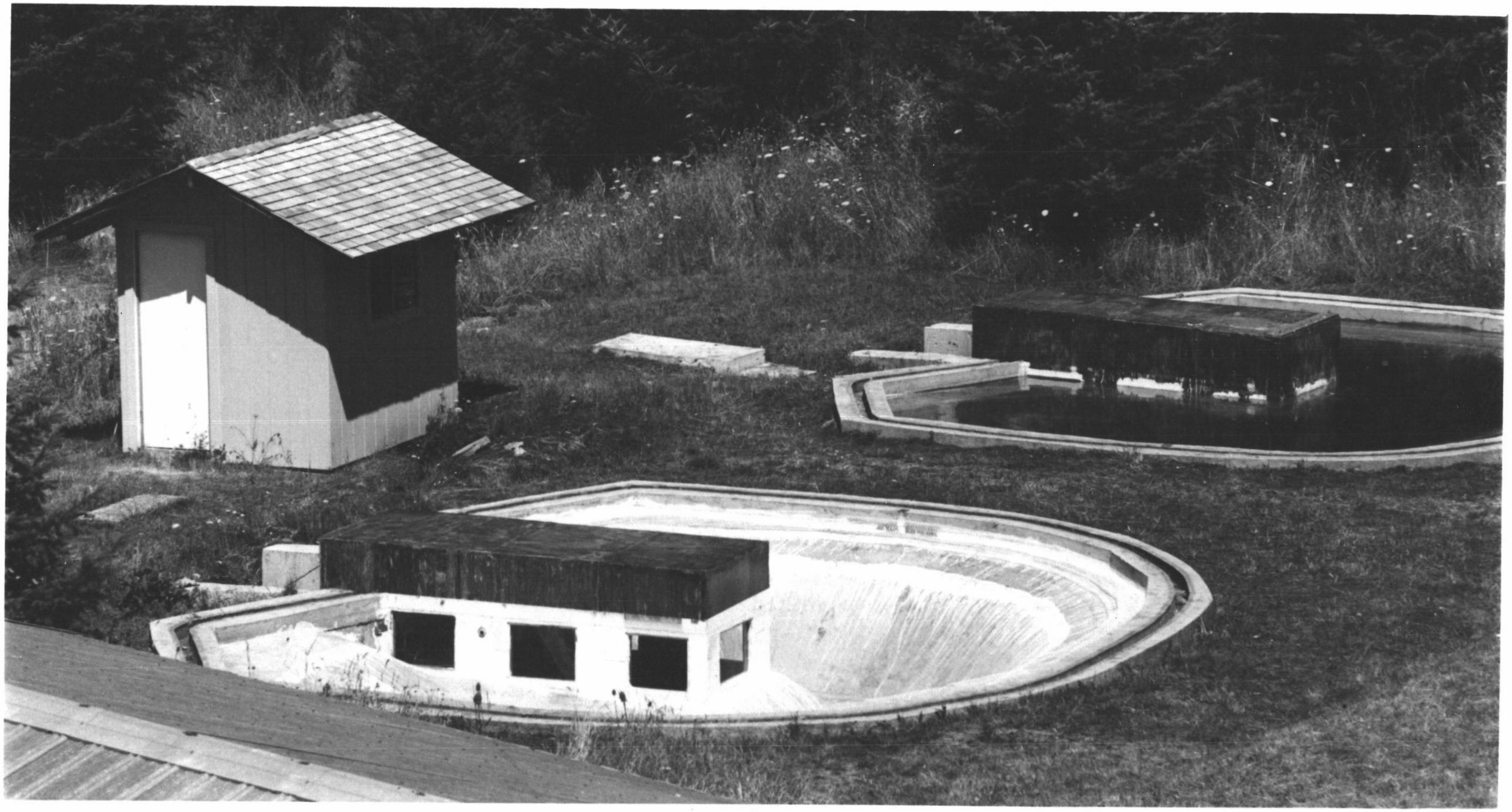

Figure 3. Photograph of the two experimental ponds used in this study.

one bass replaced in each test chamber. The remaining bass, usually two, were sacrificed, individually weighed and measured, and dried to a constant weight in an oven at 70 C for determination of the ratio of dry weight to wet weight. This ratio was used in computing the initial dry weights of all bass used in that experiment. Wet weights and lengths of all test bass were determined to the nearest 0.01 g and to the nearest 1 mm, respectively.

In order to maintain the desired experimental conditions, it was necessary to check the experimental apparatus at least twice each day and make any needed adjustments. The first daily check was made between 8:00 and 10:00 a.m. The second check was made between 4:00 and 5:00 p.m. During these checks the temperatures and water flows were recorded. The bass were fed each day between 8:00 and 10:00 a.m. for the duration of the experiment.

Mosquitofish, the only food provided bass in this study, were held without food for at least 24 hr prior to their use. The mosquitofish were then placed on an absorbent cloth pad to remove most of the adhering water, weighed in a container of water on a top-loading Mettler balance, and placed in the test chambers. Periodically throughout each experimental period, samples of mosquitofish were obtained from the stock tank and weighed before and after drying at 70 C. The mean "percent dry weight" of the samples of food (i.e., dry weight expressed as a percent of the wet weight) was determined and used in computing the dry weight of the food consumed by the test fish in each chamber.

During the course of an experiment, the individually held bass were either starved, fed one of two restricted daily rations, or fed to repletion. The three feeding levels used were maintenance (A ration), intermediate (B ration), and repletion (C ration) rations. The A ration was approximately the amount of food which would allow the bass to maintain their initial body weight during the test period. The B ration was an amount of food equal to about 5 to 10% of the body weight of the bass being fed. Bass fed at the C ration level were provided an unrestricted food supply. In all of the experiments, except experiments 4 and 5, two bass were starved and two were kept on each of the three specified rations. In experiments 4 and 5, adult bass were used and only one bass was fed at each feeding level.

At the termination of each experiment, the bass were held without food for 24 to 36 hr, after which they were removed from the test chambers, sacrificed, and individually weighed and measured. They were then dried to a constant weight at approximately 70 C, and the dry weight and percent dry weight were determined.

Pond Experiments

For each pond experiment, an appropriate number of mosquito-fish of fairly uniform size were selected from the available stock, discarding the largest and smallest individuals, and fish that appeared to be unhealthy. Once an adequate quantity of mosquitofish had been selected, a group of about 50 were removed, sacrificed, individually weighed and measured, and dried to a constant weight in an oven at approximately 70 C. The remaining fish were then weighed after removal of excess water, and the desired quantity placed in the experimental ponds.

In the first three pond experiments, the prey density decreased with time as the bass consumed the mosquitofish. In the last three experiments, mosquitofish were periodically added to the pond to replace fish that either died naturally or were consumed by bass, the rate of loss from the pond having been estimated. Thus, nearly constant prey densities were maintained during the course of these three experiments. Since the experimental ponds contained little or no food for the mosquitofish, they were fed once or twice a day a small quantity of a dry commercial guppy food, estimated to be a maintenance ration that would allow neither gain nor loss of weight during the experimental period.

Three to four days prior to the start of each pond experiment, 5 to 6 bass of a fairly uniform size were selected from the available stock and individually marked using the "cold brand" technique described by Groves and Novotny (1965) and modified by Ellis (1968). After marking, the bass were returned to the stock tank for one or two days until the brands became distinguishable. Once each individual bass in the group could be individually identified by his brand, all of the marked fish were lightly anesthetized with MS 222, weighed and measured, and 3 or 4 fish having the desired total weight were placed in the pond. The fish were marked so that individual growth rates could be obtained and the activities of individual bass could be noted.

Daily checks were made on the experimental ponds during the experiments to obtain a record of the experimental conditions and to ensure maintenance of the desired conditions. During these checks, the maximum and minimum experimental water temperatures were recorded and the water level and exchange rates adjusted if necessary. In the last experiment, a continuously recording thermograph was used to record water temperatures.

Calorimetry

A Parr oxygen bomb calorimeter (No. 1411) and appropriate, standard calorimetry and computation methods were used to determine the caloric content of a representative group of juvenile largemouth bass, having a wide range of body condition factors. The caloric content of mosquitofish tissue was also determined in order to convert grams of food consumed by bass into calories. At least two calorimetric determinations were made on each sample of fish and the mean caloric value computed.

Estimate of Assimilation

Assimilation efficiencies were determined by the iodate wet combustion method described by Brocksen (1966). After being fed, the bass were held for an appropriate period of time (24 to 48 hr) in special plexiglass test vessels, 24 cm long by 15 cm wide by 15 cm deep, containing two liters of water. Determinations were made within 72 hr after the samples of nonassimilated material were collected and frozen. The assimilation efficiency was determined for bass fed mosquitofish at three different rates and two temperatures (20 and 25 C). The total amount of oxidizable carbon initially present in each food ration was determined in conjunction with the total amount present in the nonassimilated waste products. The ratio of total oxidizable carbon assimilated to total oxidizable carbon consumed was then used as an estimate of assimilation efficiency (Davis and Warren, 1965).

Estimate of SDA

Specific dynamic action (SDA), or the energy expenditure in handling ingested food, was estimated by measuring the increase in the oxygen consumption rate of a bass following the consumption of a ration of food at 20 C. A single bass, previously unfed for 48 hr, was placed in a special respirometer, fed a measured quantity of mosquitofish, and then forced to swim at a velocity of 7.6 cm/sec. At this velocity, random activity by the fish appeared to be largely eliminated. Oxygen consumption rates of the fed bass were then determined hourly for the next 36 to 40 hr. In order to establish a metabolic rate curve for an unfed bass, oxygen consumption rate determinations were continued for another 36 hr period. A metabolic rate curve for both a fed and an unfed bass was then obtained by plotting oxygen consumption rate against time in hours. The area between these two curves was then used as an estimate of the increased metabolic rate due to SDA (Brody 1945). A polar planimeter was used to measure the area between the oxygen consumption rate curves for the fed and unfed bass.

Estimate of Standard Metabolism

An estimate of the standard metabolic rate of a bass was obtained by measuring its oxygen consumption rates at various water velocities (7.6, 10.7, 15.2, 22.9, and 29.0 cm/sec). Oxygen consumption rates were determined hourly at each velocity tested. A straight line was fitted to the lowest oxygen consumption rate obtained at each activity level and the rate at zero activity was estimated by extrapolation. The lowest oxygen consumption rate obtained at each activity level was used in fitting the curve because of the extent to which excitement can increase the rate of oxygen consumption. Smit (1965) reported that the oxygen consumption rates of goldfish, exercised at constant speed, decreased with time over a 7-hr period. This suggests that there may be a subsidence of excitement at each activity level with time.

RESULTS

Temperature Experiments

Laboratory experiments were performed to determine the effect of temperature on the relationship between food consumption and growth of bass during summer, fall, winter, and spring. The results of these experiments are presented in Table I. Initial and final wet weights and lengths of bass, wet weights of food consumed, and temperature ranges are given in Appendix I. The feeding level notation in Table 1 and Appendix I refers to a specific fish, fed at a specific rate. The notation 1-A indicates that fish number one was fed at ration A; 2-B indicates that fish number 2 was fed ration B.

Growth rates of bass are expressed in terms of weight gain or loss in milligrams per gram of mean weight of bass per day. 1/ The rate of weight gain was calculated by dividing the total dry weight gained or lost during the experimental period by the mean dry weight (i.e., average of the initial and final weights) of the individual bass. The gain in weight per gram of mean weight of bass was then divided by the length of the experiment in days. Food consumption rates, also expressed as mg/g/day, were calculated by dividing the total dry weight in milligrams of food consumed per gram of mean dry

1/ Although growth rate may be expressed in a number of ways, in this section of the text it will be used synonymously with weight gain rate, unless otherwise stated.

Table I. Initial and final weights, rates of weight gain, food consumption rates, and gross food conversion efficiencies of largemouth bass held in laboratory aquaria. All values are based on dry weights.

Experiment No. and date	Mean temperature (C)	Feeding level	Weight of bass (g) Initial	Final	Rate of weight gain (mg/g/day)	Total food consumed (mg)	Food consumption rate (mg/g/day)	Gross food conversion efficiency
Experiment 1 7/16/66	31.0	1-O	0.973	0.858	-12.55	----	----	----
		2-O	0.975	0.851	-13.58	----	----	----
		1-A	0.932	0.937	0.53	246	26.31	.020
		2-A	1.056	1.063	0.66	213	20.09	.033
		1-B	0.908	1.501	49.21	1136	94.27	.522
		2-B	0.920	1.454	44.99	1113	93.77	.480
		1-C	0.882	2.757	103.02	3899	214.23	.481
		2-C	0.935	2.910	102.70	3869	201.20	.510
Experiment 2 8/1/66	27.5	1-O	1.297	1.131	-13.67	----	----	----
		2-O	1.175	1.054	-10.85	----	----	----
		1-A	1.482	1.480	- 0.14	274	18.50	----
		2-A	1.445	1.526	5.45	286	19.25	.283
		1-B	1.327	1.936	37.32	1286	78.80	.474
		2-B	1.155	1.833	45.38	1254	83.94	.541
		1-C	1.405	3.753	91.04	4826	187.13	.487
		2-C	1.460	4.130	95.53	4931	176.42	.541
Experiment 3 8/1/66	22.9	1-O	1.081	0.951	-12.80	----	----	----
		2-O	1.265	1.131	-11.98	----	----	----
		1-A	1.103	1.125	1.97	232	20.83	.095
		2-A	1.366	1.435	4.93	276	19.70	.250
		1-B	1.383	1.967	34.87	1183	70.63	.494
		2-B	1.246	1.913	42.22	1203	76.14	.555
		1-C	1.536	3.379	74.98	3334	135.64	.553
		2-C	1.455	3.260	76.55	3534	149.87	.511

Table I. (Continued)

Experiment No. and date	Mean temperature (C)	Feeding level	Weight of bass (g) Initial	Weight of bass (g) Final	Rate of weight gain (mg/g/day)	Total food consumed (mg)	Food consumption rate (mg/g/day)	Gross food conversion efficiency
Experiment 4 8/15/66	25. 1	1-O	12. 96	12. 22	- 5. 88	----	----	----
		1-A	15. 23	16. 17	5. 99	3009	19. 17	. 312
		1-B	12. 12	14. 18	15. 67	4743	36. 07	. 434
		1-C	16. 35	19. 04	15. 20	6048	34. 17	. 445
Experiment 5 10/23/66	30. 0	1-O	16. 01	14. 73	- 8. 33	----	----	----
		1-A	16. 64	16. 39	- 1. 51	1694	10. 25	----
		1-B	16. 51	18. 12	9. 30	5247	30. 29	. 307
		1-C	15. 91	19. 24	18. 94	7977	45. 38	. 417
Experiment 6 10/23/66	26. 0	1-O	1. 589	1. 388	-13. 50	----	----	----
		1-A	1. 596	1. 493	- 6. 67	278	17. 99	----
		1-B	1. 680	2. 267	29. 74	1486	75. 28	. 395
		1-C	1. 560	3. 146	67. 40	3177	135. 02	. 499
		2-C	1. 404	3. 152	76. 73	4131	181. 34	. 423
Experiment 7 11/10/66	20. 0	1-O	1. 897	1. 829	- 3. 65	----	----	----
		2-O	2. 410	2. 258	- 6. 51	----	----	----
		1-A	2. 185	2. 195	0. 46	394	17. 99	. 026
		2-A	1. 910	1. 933	1. 20	317	16. 49	. 073
		1-B	2. 183	2. 976	30. 74	1722	66. 74	. 461
		2-B	1. 926	2. 731	34. 56	1714	73. 59	. 470
		1-C	2. 127	3. 637	52. 39	4410	153. 02	. 342
		2-C	2. 091	3. 099	38. 84	1947	75. 03	. 518
		3-C	1. 847	2. 809	41. 32	2139	91. 88	. 450
		4-C	1. 753	2. 737	43. 83	2272	101. 20	. 433

Table I. (Continued)

Experiment No. and date	Mean temperature (C)	Feeding level	Weight of bass (g) Initial	Final	Rate of weight gain (mg/g/day)	Total food consumed (mg)	Food consumption rate (mg/g/day)	Gross food conversion efficiency
Experiment 8	15.0	1-O	1.395	1.341	- 3.95	----	----	----
12/13/66		2-O	1.067	1.028	- 3.72	----	----	----
		1-A	1.356	1.510	10.75	288	20.10	.535
		2-A	1.131	1.214	7.08	258	21.99	.322
		1-B	1.194	1.513	23.56	929	68.61	.343
		2-B	1.298	1.644	23.52	885	60.16	.391
		1-C	1.215	1.495	20.66	981	72.40	.285
		2-C	1.288	1.608	22.10	1189	82.11	.269
Experiment 9	9.9	1-O	0.855	0.833	- 2.61	----	----	----
1/16/67		2-O	0.778	0.766	- 1.55	----	----	----
		1-A	0.857	0.878	2.42	89	10.25	.236
		1-B	0.784	0.852	8.31	199	24.33	.342
		2-B	0.784	0.813	3.63	73	9.14	.397
		1-C	1.001	1.116	10.86	337	31.82	.341
		2-C	0.730	0.798	8.90	257	33.64	.265
Experiment 10	15.5	1-O	0.723	0.685	- 5.40	----	----	----
2/24/67		2-O	0.813	0.774	- 4.91	----	----	----
		1-A	0.749	0.844	11.92	152	19.07	.621
		2-A	0.790	0.855	7.90	169	20.53	.385
		1-B	0.716	0.905	23.30	363	44.76	.521
		2-B	0.838	1.006	18.22	340	36.88	.494
		1-C	0.734	0.951	25.74	685	81.26	.317
		2-C	0.778	1.033	28.15	692	76.38	.369

Table I. (continued)

Experiment No. and date	Mean temperature (C)	Feeding level	Weight of bass (g) Initial	Weight of bass (g) Final	Rate of weight gain (mg/g/day)	Total food consumed (mg)	Food consumption rate (mg/g/day)	Gross food conversion efficiency
Experiment 11 2/24/67	20.2	1-O	1.012	0.937	- 7.69	----	----	----
		2-O	0.862	0.803	- 7.08	----	----	----
		1-A	0.884	0.951	7.30	205	22.33	.327
		2-A	0.964	1.013	4.95	161	16.28	.304
		1-B	0.946	1.248	27.53	592	53.97	.510
		2-B	0.893	1.214	30.46	679	64.42	.473
		1-C	0.906	1.385	41.80	1285	112.13	.373
		2-C	0.915	1.413	42.78	995	85.48	.500
Experiment 12 4/12/67	20.0	1-O	1.202	1.110	- 7.96	----	----	----
		2-O	1.193	1.130	- 5.42	----	----	----
		1-A	1.170	1.173	0.26	188	16.04	.016
		2-A	1.309	1.369	4.48	181	13.52	.331
		1-B	1.156	1.464	23.51	724	55.27	.425
		2-B	1.323	1.670	23.18	782	52.24	.444
		1-C	1.184	1.915	47.16	2095	135.16	.349
		2-C	1.191	2.088	54.70	2146	130.85	.418
Experiment 13 4/12/67	14.8	1-O	1.113	1.053	- 5.54	----	----	----
		2-O	1.139	1.057	- 7.47	----	----	----
		1-A	1.051	1.084	3.09	161	15.07	.205
		2-A	1.192	1.202	0.84	108	9.02	.091
		1-B	1.231	1.516	20.74	452	32.09	.630
		2-B	1.082	1.342	21.45	513	42.33	.507
		1-C	1.155	1.613	33.09	1194	86.27	.384
		2-C	1.172	1.578	29.53	1174	85.38	.346

Table I. (Continued)

Experiment No. and date	Mean temperature (C)	Feeding level	Weight of bass (g) Initial	Final	Rate of weight gain (mg/g/day)	Total food consumed (mg)	Food consumption rate (mg/g/day)	Gross food conversion efficiency
Experiment 14 5/1/67	25.3	1-O	1.290	1.153	-11.21	----	----	----
		2-O	1.260	1.139	-10.08	----	----	----
		1-A	0.861	0.893	3.65	227	25.88	.141
		2-A	1.140	1.152	1.05	206	17.98	.058
		1-B	1.338	1.596	17.59	702	47.85	.368
		2-B	1.324	1.652	22.04	792	53.23	.414
		1-C	1.062	2.269	72.45	2016	121.01	.599
		2-C	1.036	2.347	77.48	2241	145.95	.531
Experiment 15 7/5/67	20.0	1-O	1.511	1.413	- 6.70	----	----	----
		2-O	1.944	1.808	- 7.25	----	----	----
		1-A	1.799	1.875	4.14	284	15.46	.268
		2-A	1.801	1.846	2.47	301	16.50	.150
		1-B	1.629	2.051	22.93	913	49.62	.462
		2-B	1.595	2.063	25.59	943	51.56	.496
		1-C	1.828	3.147	53.01	3119	125.36	.423
		2-C	1.698	2.935	53.39	3244	140.01	.381

weight of bass by the length of the experiment in days. Gross food conversion efficiency, the efficiency of conversion of food into fish flesh, was calculated by dividing the weight gain by the weight of food consumed.

Presented in Fig. 4 is the relationship between food consumption rate and growth rate of bass during summer, as affected by exposure to constant water temperatures of 31, 28, 23, and 20 C. The food consumption and growth rates of bass fed the repletion ration decreased with a decrease in temperature. Bass fed to repletion and held at 31 C consumed about 215 mg/g/day, whereas at 20 C they consumed only about 140 mg/g/day. The food consumption rate at which the bass neither gained nor lost weight (maintenance level) decreased with a decrease in temperature. The maintenance ration for bass was approximately twice as high at 31 C as at 20 C.

The relationship between food consumption and growth of bass exposed to experimental temperatures of about 25, 20, and 15 C during fall and spring are presented in Fig. 5 and 6, respectively. It can be seen that a decrease in temperature from 25 to 15 C resulted in a decrease in the maximum food consumption and growth rate of bass fed to repletion during both seasons. The maintenance ration also decreased with a decrease in temperature during both seasons, as did the rate at which unfed bass lost weight. Fish held without food at 20 C during fall, however, did not lose as much weight as

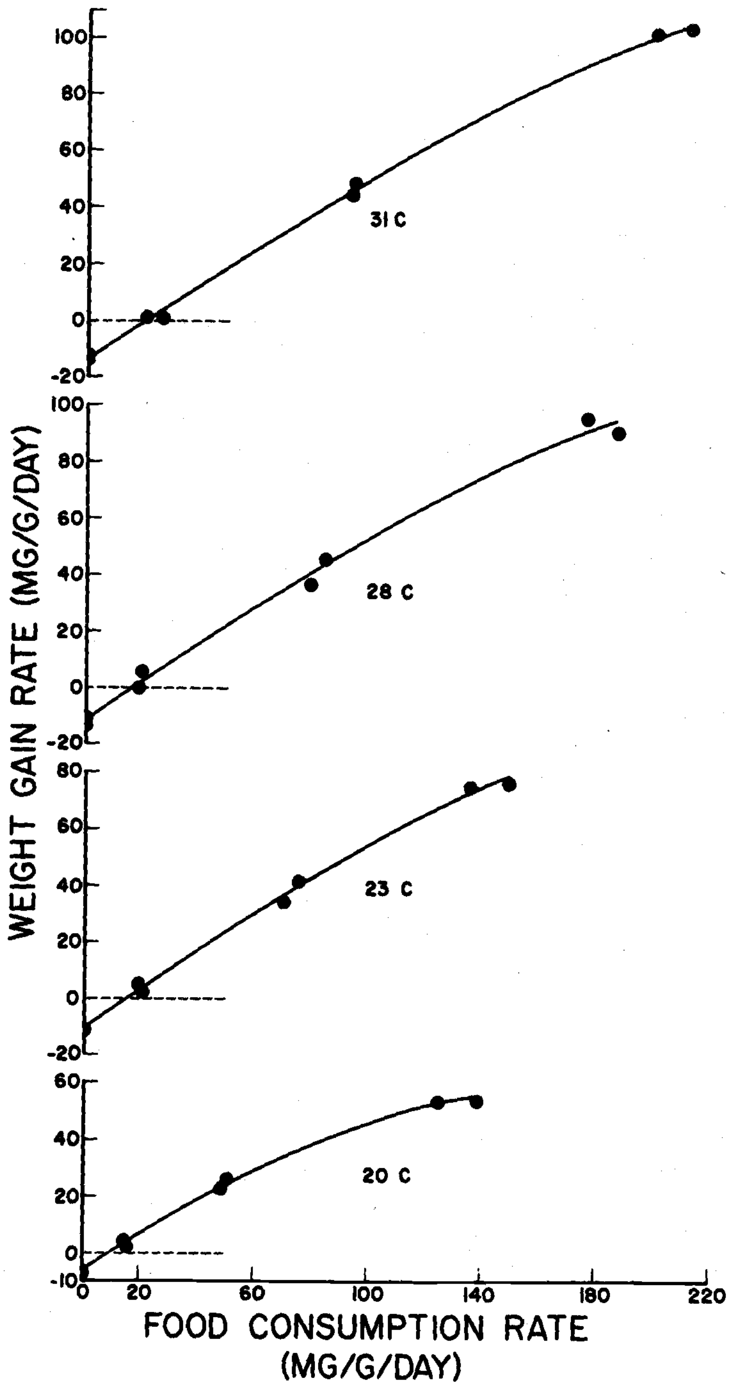

Figure 4. The relations between food consumption and growth rates of juvenile largemouth bass held individually in glass aquaria and either unfed, fed one of two restricted rations, or fed to repletion with mosquitofish for 10 days at 23, 28, and 31 C during summer, 1966 and at 20 C during summer, 1967.

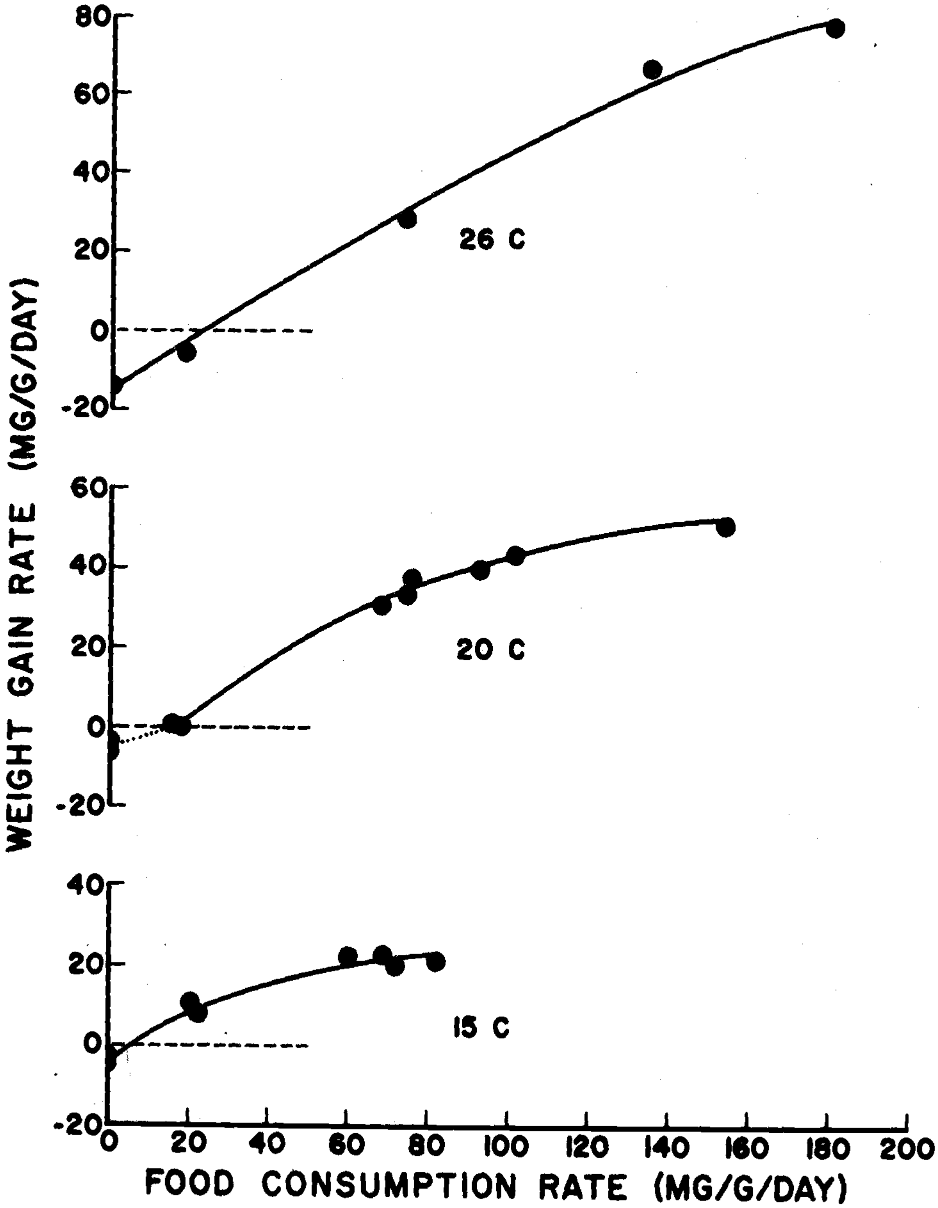

Figure 5. The relationship between food consumption rate and growth rate of juvenile largemouth bass held individually in glass aquaria for 10 days at 15, 20 and 26 C during fall, 1966. A dotted line was drawn from the maintenance food consumption rate level to the zero level on the 20 C curve because the fish did not lose as much weight as expected on the basis of the rest of the data.

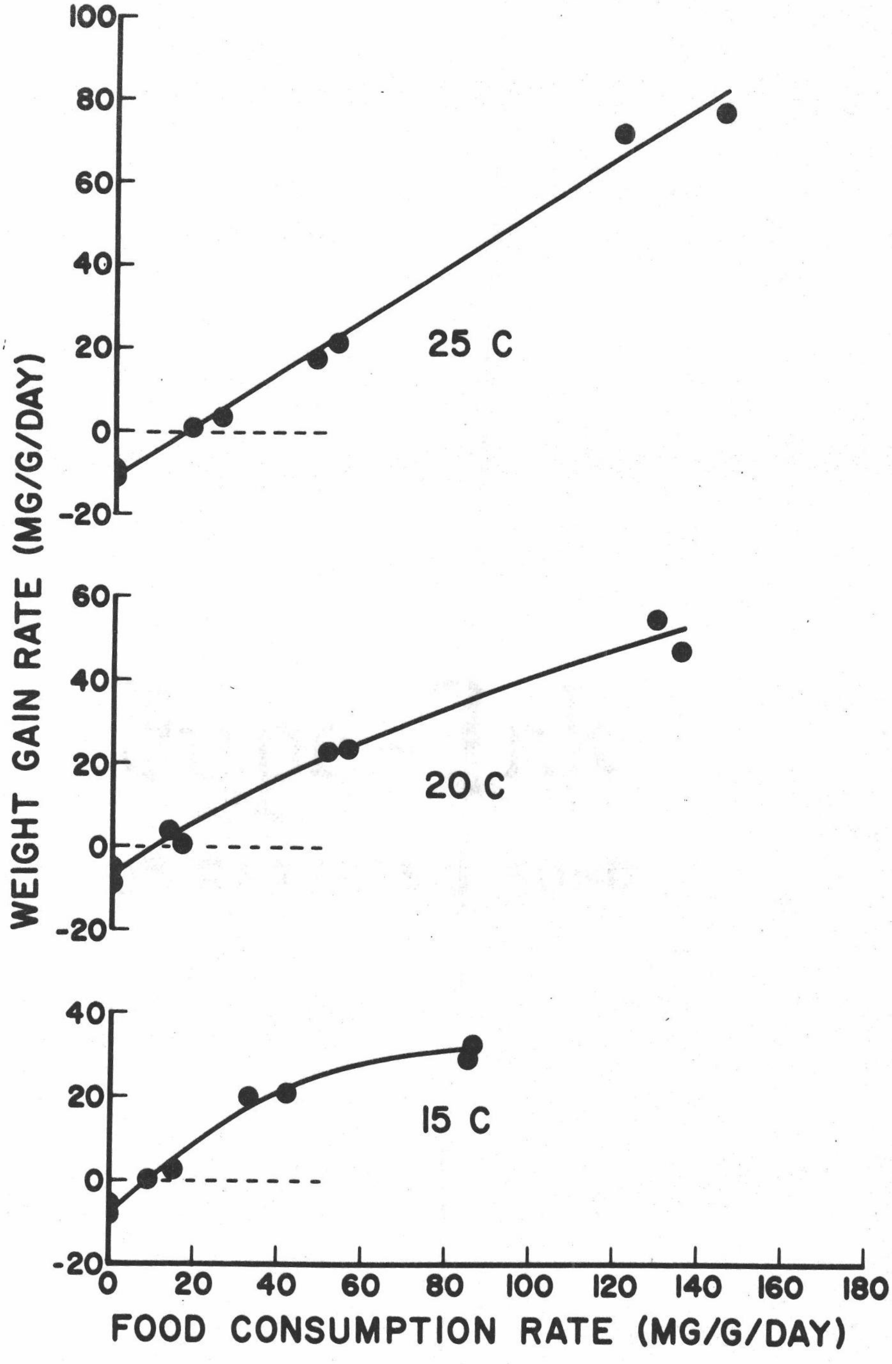

Figure 6. The relationship between food consumption rate and growth rate of largemouth bass during spring, 1967. The bass were held individually in glass aquaria at 15, 20 and 25 C and either held without food, fed one of two restricted rations, or fed to repletion with mosquitofish.

would be expected in view of other data obtained for bass held at 20 C during summer, spring, and winter. A dotted line was fitted to the points representing negative growth rates of unfed fish (Fig. 5) because it is not known why these fish did not lose more weight, and the data are, therefore, questionable.

The relationship between food consumption and growth of bass held at 20, 15,and 10 C during winter is presented in Fig. 7. The maximum food consumption rate of bass fed to repletion decreased from about 110 mg/g/day at 20 C to about 35 mg/g/day at 10 C. Correspondingly, the same change in temperature resulted in a reduction in growth rate from about 45 mg/g/day to about 10 mg/g/day. The maintenance ration was found to be approximately three times as high at 20 C as at 10 C.

The curves relating food consumption and growth rates at different temperatures for each season of the year (Fig. 4, 5, 6,and 7) are presented in Fig. 8 to facilitate comparison of the relationships. In general, bass fed to repletion consumed more food and grew more rapidly at higher temperatures than at lower temperatures, regardless of season. As previously mentioned, the maintenance ration and rate of weight loss during starvation decreased with decreasing temperature.

The curves relating food consumption to growth of bass held at the lower temperatures (during fall, winter, and spring) intersect

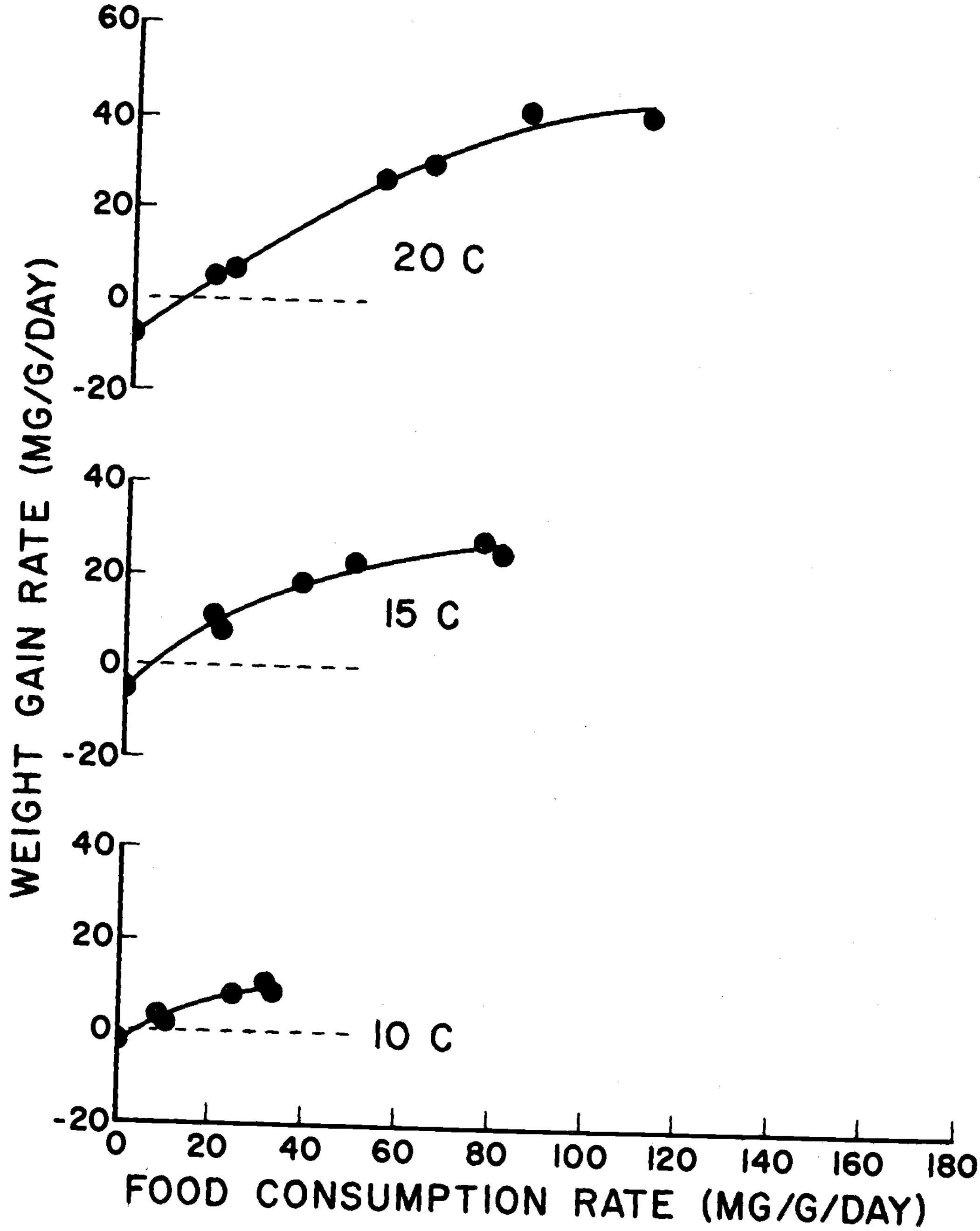

Figure 7. The growth rate of juvenile largemouth bass in relation to food consumption rate during winter, 1967. The bass were held individually in glass aquaria for 10 days at 10, 15 and 20 C and were held without food, fed one of two restricted rations, or fed to repletion with mosquitofish.

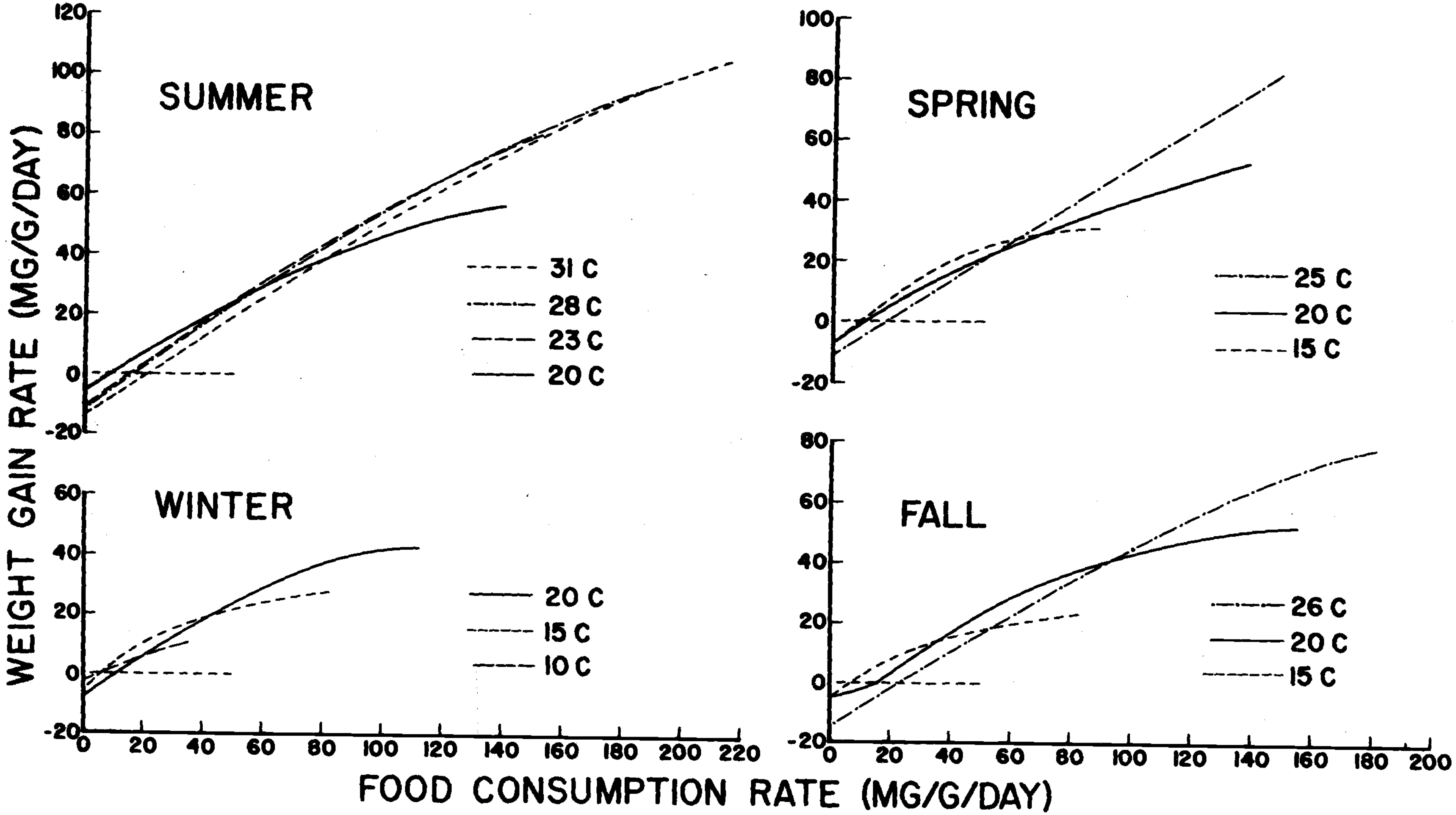

Figure 8. The relationship between food consumption rate and growth rate of juvenile largemouth bass held at various temperatures during summer, fall, winter and spring, 1966-67. The data was obtained from Figures 4, 5, 6, and 7 to facilitate easier comparison.

those representing food consumption and growth of bass at higher temperatures (Fig. 8). At any food consumption rate above the rate at which the curves cross, the gross efficiency (*i. e.*, ratio of growth to food intake) is greater at the higher temperature than at the lower temperature. During the summer experiments this same general relationship was observed, except that the food consumption-growth rate curves obtained at 23 and 28 C did not intersect the 31 C curve.

Food consumption and growth rate relationships for bass held under continuous light conditions at 20 C during summer, fall, winter, and spring suggest that season has little effect on this relationship (Fig. 9). The bass consumed food and grew at nearly equal rates in the different seasons, and the maintenance ration and rate of weight loss of unfed fish appear to be also uniform. Bass reared during winter exhibited somewhat lower food consumption and growth rates when fed to repletion than did those reared during the other seasons of the year, but this difference may have been fortuitous.

The curves presented in Fig. 10 show the relationship between gross food conversion efficiency and food consumption rate at different temperatures. The gross efficiency of food conversion is determined by dividing the amount of tissue elaborated as growth by the total amount of food consumed. As can be seen in Fig. 10, at low food consumption rates, bass converted food more efficiently at 15 C than at 20 C, or above. At higher food consumption rates, however,

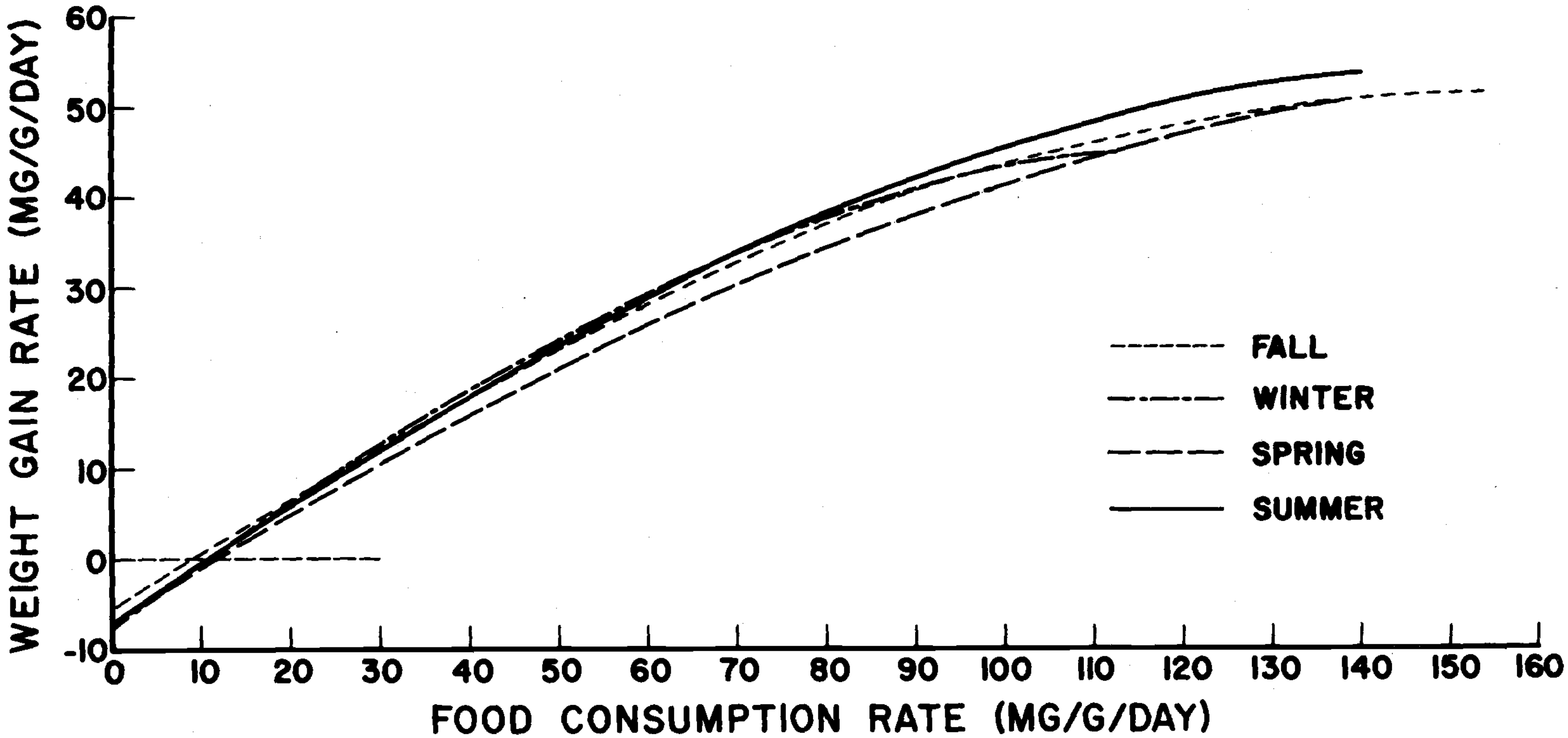

Figure 9. The relationship between food consumption rate and growth rate of juvenile largemouth bass held individually in glass aquaria at 20 C during spring, summer, fall, and winter, 1966-67. The data was taken from the 20 C curves presented in Figures 4, 5, 6, and 7.

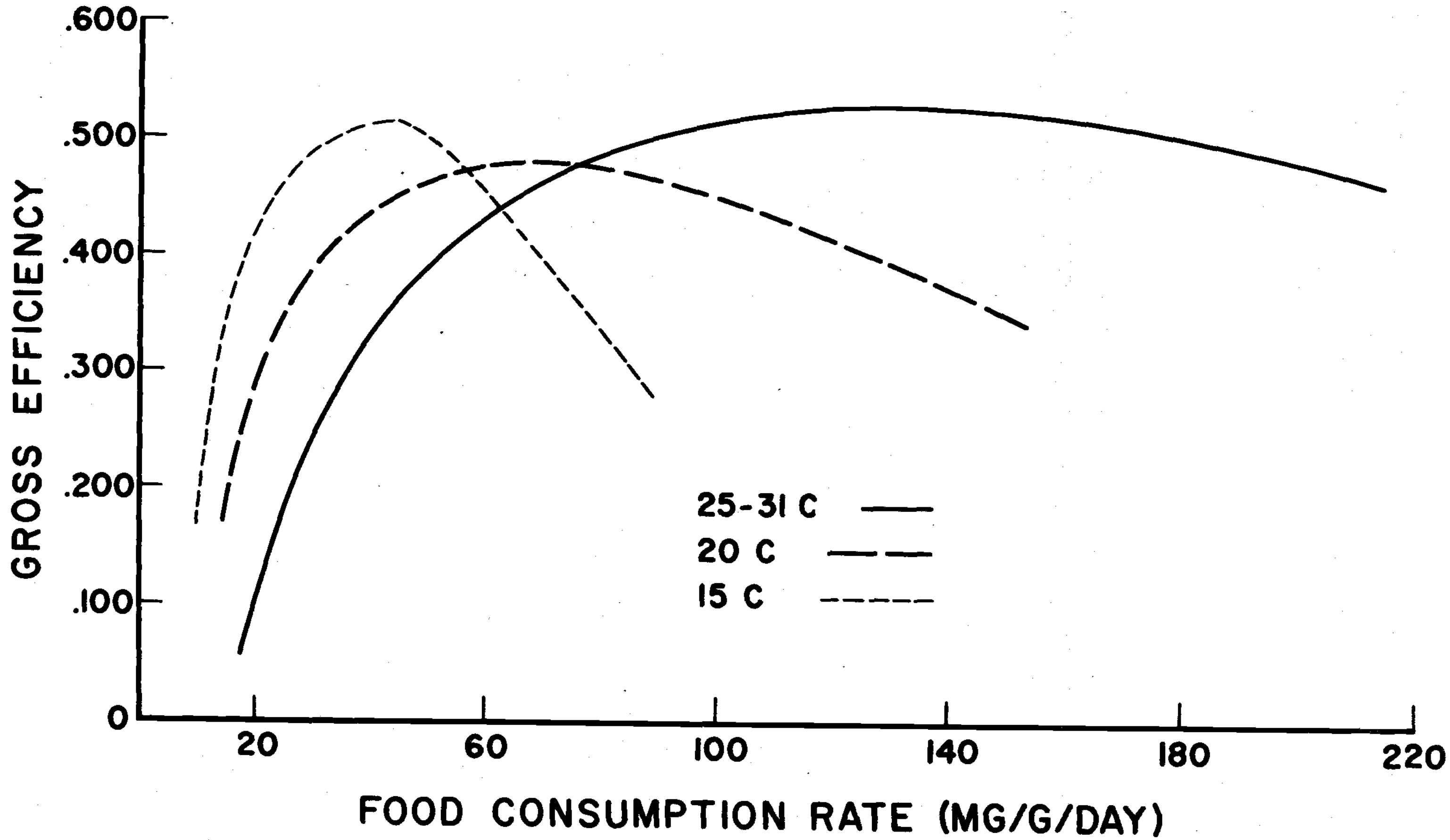

Figure 10. The relationship between gross food conversion efficiency and food consumption rate of juvenile largemouth bass at temperatures of 15, 20, and 25-31 C for all seasons of the year, 1966-67. The data were taken from the relationship between food consumption rate and growth rate of bass presented in Table I and in Figures 4, 5, 6, and 7.

bass were more efficient at the higher temperatures (20 C and above). The higher the temperature the broader was the range of feeding rates permitting high efficiency and the more gradual the decline in efficiency at high food consumption rates. Bass held at 15 C exhibited a peak efficiency of 0.52, but this high efficiency was restricted to a very narrow range of food consumption rates. The peak efficiency for bass at 20 C was about 0.46. The range of food consumption rates over which the efficiency remained high was much broader at 20 C than at 15 C. This range for bass held at temperatures ranging from 25 to 31 C was very broad and the peak efficiency was about 0.54.

The relationships between food consumption and growth of bass weighing about 60 g (Table I) and held at 25 and 30 C during summer are presented in Fig. 11. Although the large bass fed to repletion consumed more food per day than small bass, the rate of food consumption per unit of body weight was much lower. The large bass were able to maintain their body weight at a lower food consumption rate than were the small bass reared at the same temperature. The maintenance rations for large bass held at 25 and 30 C were 10 and 14 mg/g/day, respectively (Fig. 11), whereas the maintenance rations for smaller bass held at 23, 28 and 31 C were 15, 17 and 20 mg/g/day, respectively (Fig. 4). The rates of weight loss for unfed large bass were less than those for unfed small bass held at the same temperatures. In contrast, the maximum growth rate observed for

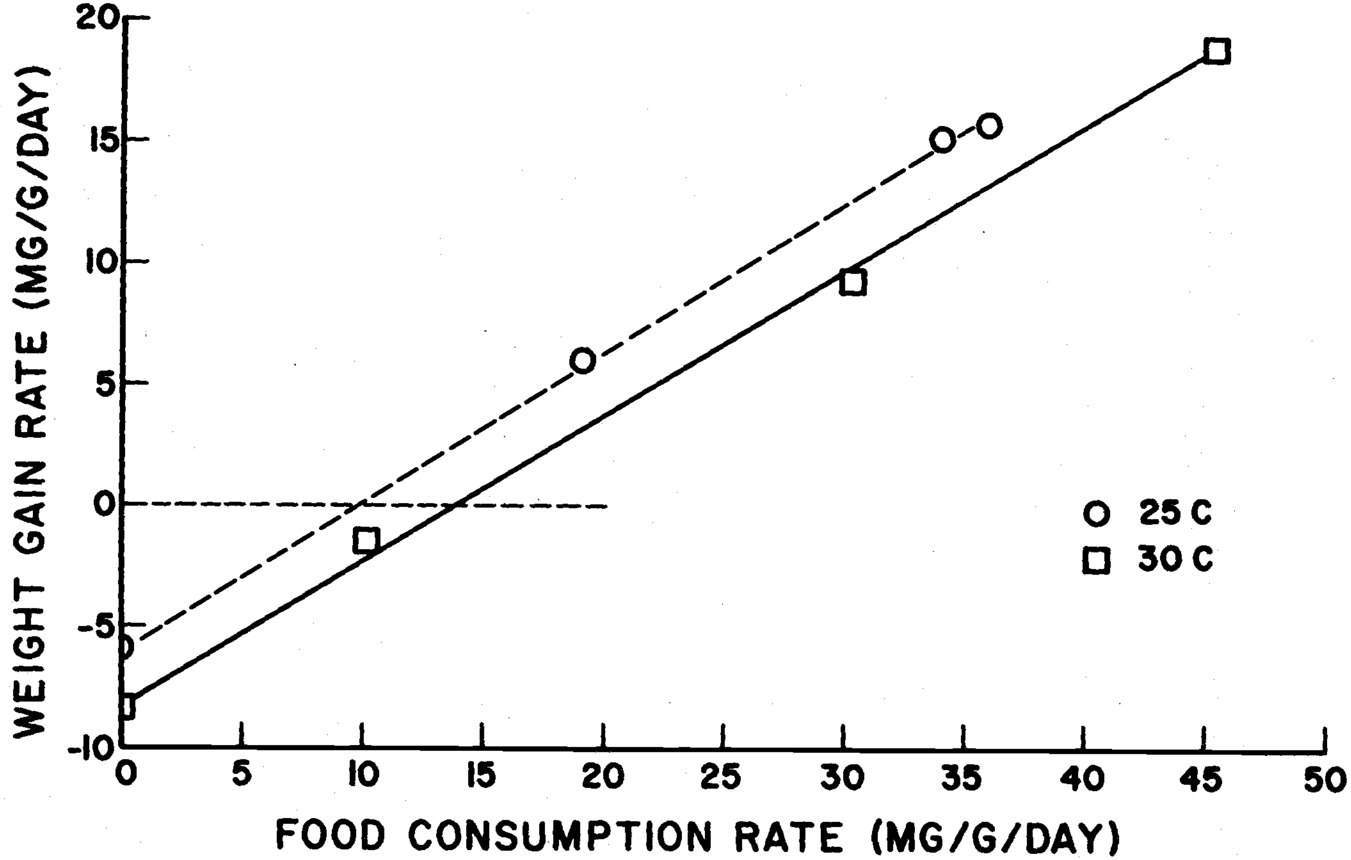

Figure 11. The growth rate of adult largemouth bass in relation to food consumption rate. The bass were held for 10 days in glass aquaria at 25 and 30 C and either unfed, fed one of two restricted rations each day, or fed to repletion with mosquitofish.

small bass was much higher than that exhibited by large bass. At comparable food consumption rates, however, food conversion efficiencies exhibited by the larger bass were slightly higher than those of the smaller bass.

Pond Experiments

Food consumption and growth rates were determined for juvenile largemouth bass held in the experimental ponds for 10-day periods during summer at temperatures averaging about 21 C, and confronted with widely varying densities of prey (mosquitofish). The food consumption and growth rates of bass increased with an increase of prey density, nearly reaching a plateau at the highest prey density provided (Table II & III). Wet weights, lengths, and condition factors for individual bass and temperature data are given in Table IV.

In the pond experiments, an attempt was made to expose a nearly constant bass biomass to various prey densities (106 and 272 cal/m^2) to better understand the influence of prey density on predator food consumption and growth rate. As the prey density increased over the range of densities studied, the food consumption rate of bass also increased, with a corresponding increase in growth rate.

In order to determine if the wire cylinders were effective in providing escape cover for the mosquitofish, an experiment was performed in which two ponds were in operation simultaneously, one

Table II. Caloric and wet weight values for juvenile largemouth bass held in experimental ponds for 10-day periods and provided with various densities of mosquitofish during summer, 1967

Experiment	Caloric value [1]			Wet weight in grams			Growth rate [2]	
	Initial	Final	Increase	Initial	Final	Increase	mg/g/day	cal/kolocal/day
A	48,434	58.781	10,347	36.6	43.4	6.8	16.9	19.3
B	63,242	71,894	8,652	49.4	57.1	7.7	14.5	12.8
C [3]	64,196	98,298	34,298	51.6	74.3	22.7	36.0	42.2
D	69,150	75,110	5,960	53.2	59.0	5.8	10.4	8.2
E	60,367	61,845	1,478	48.1	49.9	1.8	3.8	2.4
F	58,547	72,304	13,757	45.5	55.1	9.6	19.0	21.0

1/ The caloric value determinations are estimates based on the condition factors of the bass (Table IV).

2/ Growth rates are expressed as milligrams per gram of mean weight of bass per day and as calories per mean kilocalorie of bass per day.

3/ The wire cylinders used as cover to protect the prey (mosquitofish) were not present in this experiment.

Table III. Caloric and wet weight values for mosquitofish placed in experimental ponds at various densities for 10-day periods, providing a source of food for juvenile largemouth bass during summer, 1967.

Experiment	Mean mosquitofish density		Mean wet weight of mosquitofish [1/]		Standard deviation		Food consumed		Food consumption rate [2/]	
	(cal/m^2)	(g/pond)	Initial sample (g)	Final sample (g)	Initial	Final	(g)	(cal)	(mg/g/day)	(cal/kilocal/day)
A	238	208	.197	.185	.082	.071	24.8	29,640	62.08	55.30
B	186	168	.199	.191	.069	.063	27.9	34,840	52.85	51.56
C	180	159	.184	.167	.048	.039	62.5	74,350	99.33	89.58
D	137	120	.141	.137	.059	.052	27.5	30,670	49.12	42.52
E	112	106	.146	.149	.072	.059	18.6	21,770	37.94	35.62
F	311	272	.131	.137	.062	.053	38.5	41,330	76.44	63.17

1/ A sample size of 50 fish was used for each determination.

2/ Food consumption rates are expressed as milligrams per gram of mean weight of bass per day and as calories per mean kilocalorie of bass per day.

Table IV. Initial and final wet weights. lengths, and condition factors of individual largemouth bass placed in experimental ponds and provided various densities of mosquitofish

Experiment and date	Temperature (C) Mean	Range	Wet weight (g) Initial	Final	Length (cm) Initial	Final	Condition factor 1/ Initial	Final
A	18.1	12.4-27.1	9.0	11.0	9.1	9.5	1.20	1.28
(5/29/67)			7.3	8.3	8.6	8.9	1.15	1.18
			11.3	13.7	9.8	10.2	1.20	1.29
			8.9	10.4	8.8	9.3	1.31	1.29
B	20.5	13.0-31.3	18.9	21.1	11.8	12.3	1.15	1.13
(6/13/67)			16.1	18.7	11.4	11.9	1.09	1.11
			14.4	17.4	10.8	11.4	1.14	1.17
C	20.5	13.0-31.3	18.7	27.1	12.2	12.8	1.03	1.29
(6/13/67)			16.8	26.1	11.8	12.6	1.02	1.31
			16.1	25.1	11.5	12.4	1.06	1.32
D	22.6	15.2-30.6	17.6	20.1	11.2	11.7	1.25	1.26
(7/11/67)			13.7	14.8	10.5	10.9	1.18	1.14
			10.6	11.8	10.0	10.4	1.06	1.05
E	23.3	17.0-31.8	14.6	15.2	11.0	11.2	1.10	1.08
(7/30/67)			21.0	22.4	12.1	12.4	1.19	1.17
			12.5	12.4	10.5	10.6	1.08	1.04
F	21.0	15.8-29.2	12.2	13.5	10.2	10.6	1.15	1.13
			10.5	13.8	9.6	10.4	1.19	1.23
			11.6	12.7	10.0	10.3	1.16	1.16
			11.2	15.2	9.9	10.6	1.15	1.28

1/ Condition factors were computed by the following formula:

$$\text{Condition factor} = \frac{\text{weight}}{(\text{length})^3}$$

with the wire cylinders in place and one without them. Approximately equal weights of bass and equal weights of mosquitofish were placed in the two ponds (in experiments B and C). The food consumption and growth rates of bass in the pond provided cover were approximately 52.85 and 14.5 mg/g/day, respectively, whereas in the pond without wire cylinders the food consumption and growth rates were higher at 99.33 and 36.0 mg/g/day, respectively (Tables II and III).

The results of assimilation efficiency experiments for bass held at two temperatures and fed once at three different feeding levels are presented in Fig. 12. As can be seen in this figure, the assimilation efficiency decreased as the food consumption increased. The 20 C assimilation efficiency curve was extrapolated to a higher food consumption value (dashed line) because it was necessary to estimate assimilation efficiencies at higher food consumption rates than were tested in the assimilation tests. Assimilation efficiency appeared to be affected by temperature, with a lower temperature resulting in a lower assimilation efficiency.

The relationships between prey density and food consumption, growth, assimilation, and respiration rates of largemouth bass held in experimental ponds are presented in terms of energy in Fig. 13. The difference between the initial and final mosquitofish weights for each experiment was taken to be the weight of food consumed by bass, since there was no statistical difference (at 95% level) in the mean

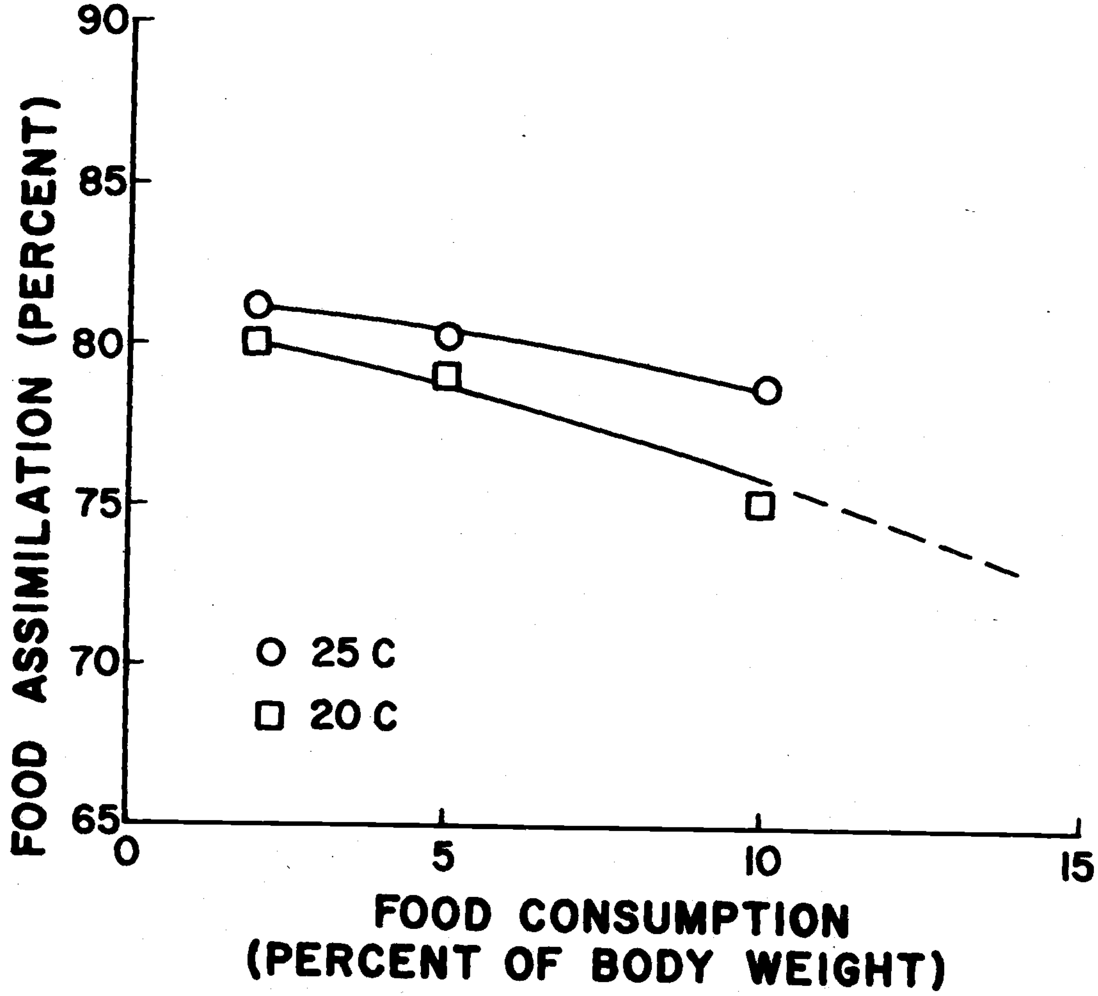

Figure 12. Food assimilation efficiency, in percent, for juvenile largemouth bass held at 20 and 25 C and fed at three different food consumption levels. The bass were fed only once at each level. Food consumption rates are based on dry weights and are expressed as percent of body weight.

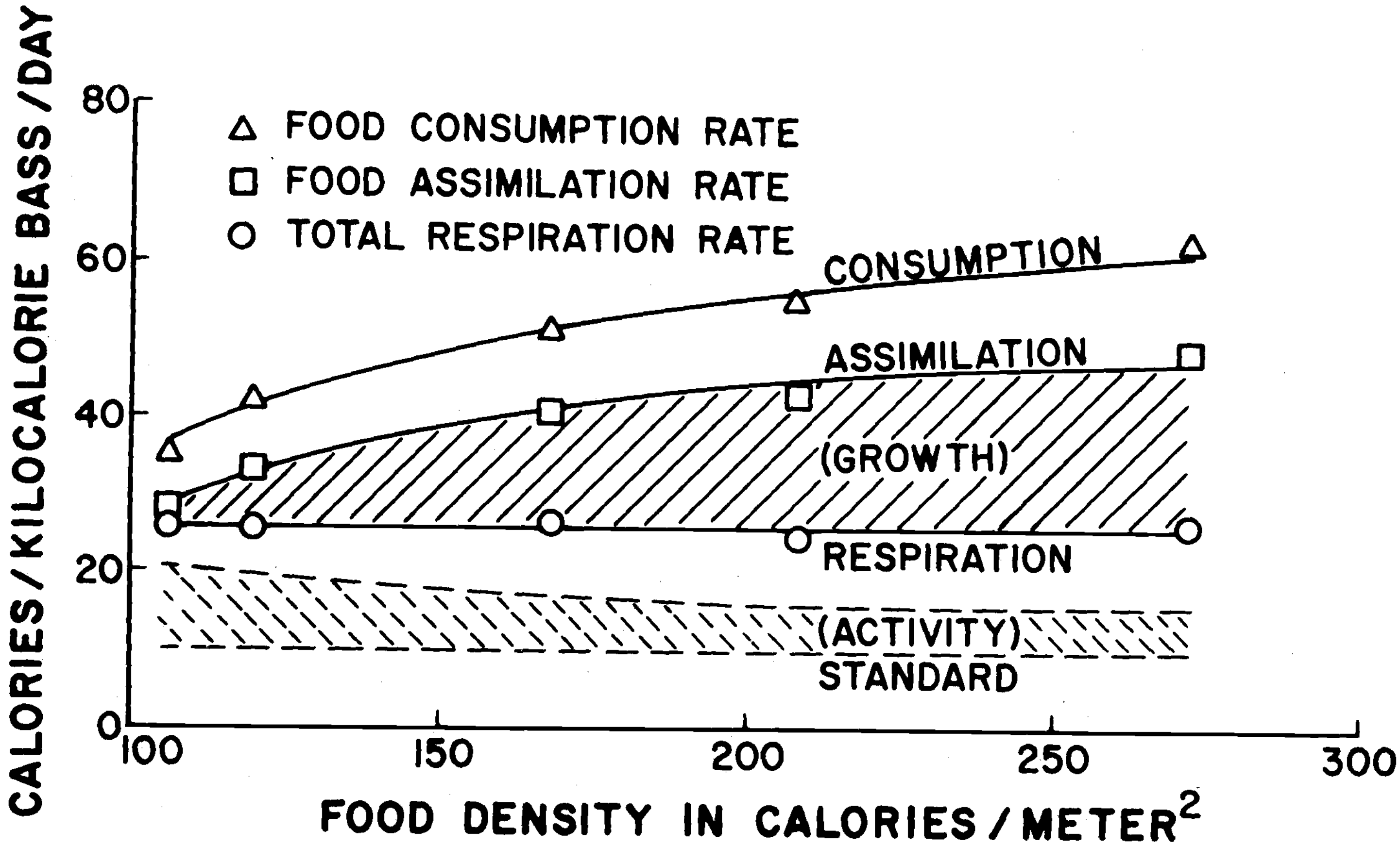

Figure 13. An energy budget depicting the fate of all energy consumed as food by juvenile largemouth bass held for 10 days in experimental ponds and confronted with widely varying densities of prey (mosquitofish) during summer, 1967. The mean temperatures for the various experiments ranged between 18 and 23 C.

individual size of the mosquitofish between the start and finish of each experiment. Weights of mosquitofish which were found to have died in the ponds from causes other than consumption by bass were subtracted from the difference between the initial and final mosquitofish weights. The amount of food consumed in grams was then converted to calories (Table III). Growth rates were obtained by determining the condition factor for each bass from length and weight measurements taken at the beginning and end of each experiment and using a curve relating condition factor and calories per gram wet weight of bass to obtain total calories for each bass at the beginning and end of each experiment (Appendix IV). The change in total calories of each individual bass during an experiment was then measured. The growth rate of the entire bass population for each experiment was determined by summing the individual gains (in calories) of all the bass and dividing this value by the mean of the initial and final caloric values (expressed in kilocalories) of all bass present and the length of the experiment in days (Table II). Food assimilation efficiencies for the various food consumption rates were obtained by interpolation from the curve relating food consumed and assimilation efficiency at 20 C, presented in Fig. 12. It should be noted that the test bass used to determine assimilation efficiency were provided with food only once, whereas bass in the experimental ponds were probably consuming food throughout the day. Specific dynamic action was taken to be 15.2 percent of the total energy consumed, regardless of the food consumption rate, since this value was the only one determined for SDA in this study (Appendix III). Standard metabolism was estimated to be about 10 cal/kilocalorie bass/day by projecting to the zero activity level a straight line representing the relationship between oxygen consumption rate and activity as suggested by Brett (1964) (Appendix II).

The food consumption and growth rates of bass in the experimental ponds increased with an increase in prey density, nearly reaching a plateau at the highest food density provided (Fig. 13). The energy cost for activity decreased as prey density increased. Specific dynamic action is shown to increase with increased prey density due to consumption of larger amounts of food by bass when food becomes more readily available. It is interesting to note that the total cost of respiration remained nearly constant at all food densities tested.

Presented in Fig. 14 is an energy budget for bass held in individual glass aquaria at 20 C during spring and fed at various constant rates for 10 days (Experiment 12). The growth rate of bass increased with increased food consumption rate, reaching its highest level at the highest food intake rate. Total respiration costs increased with increasing food consumption rate, being highest (about 27-28 cal/kilocalorie bass/day) at the highest level of energy intake.

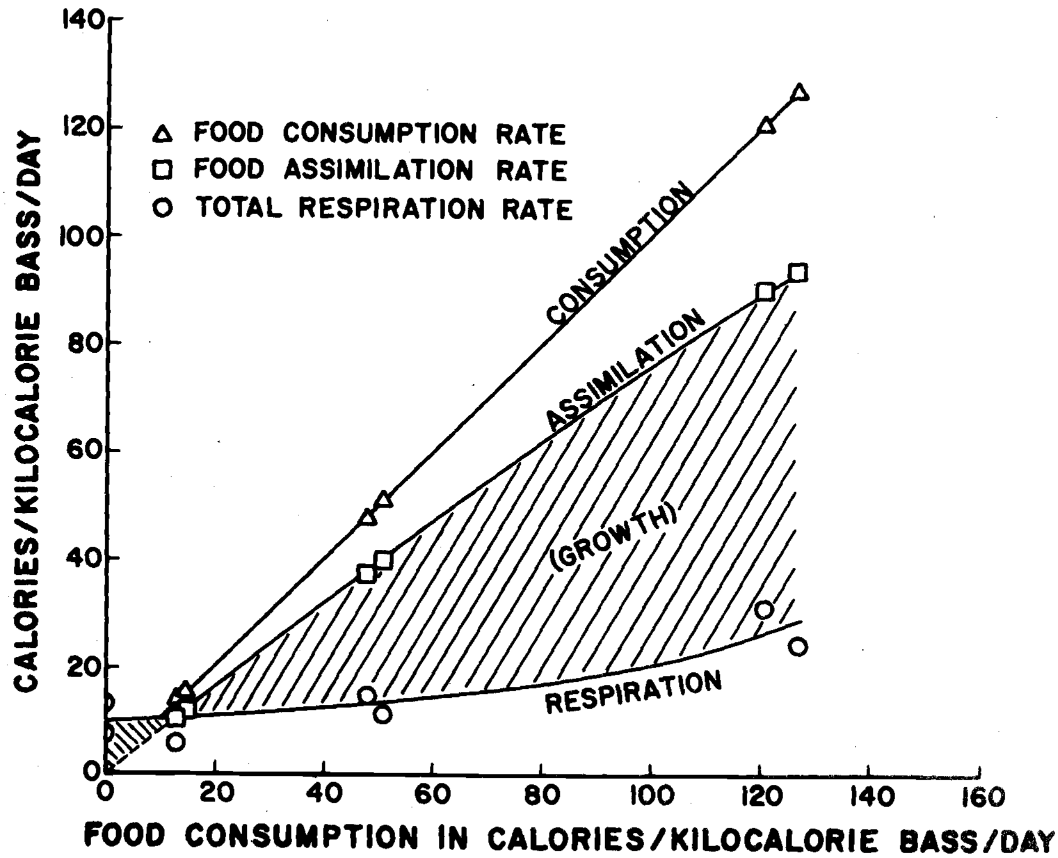

Figure 14. The relationships between food consumption rate and assimilation, growth, and respiration rates for juvenile largemouth bass held at 20 C in individual test chambers in the laboratory and either not fed or fed at specific rates. Assimilation efficiencies for bass fed at high food consumption rates were obtained by extrapolating the 20 C assimilation efficiency curve presented in Figure 12.

A loss of energy resulting from the use of body tissue by the bass is illustrated by the hatched triangular-shaped area at the lower left hand corner of Fig. 14. An unfed bass must use its body tissue exclusively to maintain metabolic processes. As food intake increases, and finally approaches a maintenance requirement, the amount of energy lost through the use of body tissue decreases. The remainder of the energy (below the hatched area) would come from food consumption.

DISCUSSION

In studying the relations between a predator and prey it is important to evaluate the basic relationships involved in the production of the desired species. Brocksen et al. (1968) suggest that the rate of production of a predator species is dependent on the interactions between predator biomass, prey availability, and predator growth rate. In this study, the effect of prey availability on predator growth rate was investigated, while the predator biomass was maintained at a nearly constant level.

A bioenergetic approach to this problem was used because of the relatively clear relationships involved in such a point of view. Food consumed by a fish is either assimilated or passes out as feces. The assimilated energy from food intake which exceeds that amount necessary to satisfy total respiration costs (total metabolic rate) and any other energy use or loss, is available for growth. By using the bioenergetic approach, all of the necessary relationships involved can be expressed in calories and, therefore, reduced to a common term.

One of the most interesting features of the bioenergetic budget for bass in the experimental ponds is the remarkable stability of the total metabolic rate (Fig. 13). Even though food consumption and growth rates increase with increased prey densities, the estimated total metabolism appeared to remain nearly constant at about 26-27 cal/kilocalorie bass/day. This somewhat surprising result does not agree with the findings reported by Brocksen et al. (1968) on cutthroat trout and reticulate sculpins held in laboratory streams. They reported that the total metabolic rate of both species of fish increases with increased food density, primarily because of increased energy expenditure for DSA. However, the data on cutthroat trout which they advance to support this conclusion is less than convincing.

If, instead of measuring food consumption, I had used the growth rates of bass obtained in the present pond study to estimate food consumption rates, following the procedure of Brocksen et al. (1968), the estimated total metabolic rates would also have increased with increased food density. This suggests, I feel, that the relation between food consumption and growth rates observed in laboratory aquaria may have somewhat limited value in deriving food consumption rates from growth rates observed under the nearly natural conditions of our ponds. Ivlev (1961) working with his model suggested that the respiration rate of the plankton-feeding *Alburnus alburnus* would decrease with increased food density, but did not take into account increased energy expenditure for SDA.

The cost of food handling or energy expenditure for SDA obtained in this study (15.2%) may be too high or even too low, primarily because SDA was measured for only one bass at one feeding level. Cohn (1963), working with rats, reported that the energy expenditure for SDA may vary with the size of the meal and that this may cause the energy cost of SDA to vary as food ration varies. Various successive rations over a period of several days may also influence SDA. If the energy expenditure value for SDA used in this study is in error, so also is the estimated energy expenditure for activity, since the latter is obtained by difference. However, such an error would not alter the estimate of total metabolic rate.

The total metabolic rate for bass fed to repletion and held in the laboratory aquaria at 20 C was estimated to be about 27-28 cal/ kilocalorie bass/day (Fig. 14). This suggests that at a temperature of approximately 20 C the total metabolic rate for bass held in aquaria and fed to repletion is nearly the same as that for bass in the experimental ponds, regardless of the prey density. It is also interesting to note that food consumption and growth rates of bass were more than doubled in the pond experiment in which prey cover was removed, yet the total metabolic rate was found to be approximately 26 cal/kilocalorie bass/day.

The total metabolic rate for bass held in aquaria and fed at various levels did not remain constant, but rather increased as rations increased to the maximum food consumption rate. This increase in total metabolic rate with ration may be explained by noting that the rate of energy expenditure for activity even at a low feeding level must have been very low, the combined energy expenditure for activity and SDA and therefore also the total metabolic rate could be maximal only when the bass were fed to repletion. In fact, it seems quite likely that bass offered little or no food in aquaria expended less energy for activity than the bass fed to excess, which had to expend more energy in capturing the food offered than did bass receiving little food.

The total metabolic rate estimated for bass in the experimental ponds (26-27 cal/kilocalorie bass/day) appears to be somewhat below the metabolic rate observed for bass forced to swim in an activity respirometer at a nearly maximum sustainable speed (32 cal/kilocalorie bass/day). It would seem, then, that bass in the ponds had the ability to increase their metabolic rate, but for some reason they did not do so. It appears, therefore, that the total metabolic rate of these bass was limited by some factor (other than food density), which at present is unknown, although there is some evidence to suggest that this factor may have been the dissolved oxygen concentration of the water.

Stewart et al. (1967) and Fisher (1963) have shown that the food consumption and growth rates of bass and coho salmon fed to excess decreased with a decrease in oxygen concentration below air-saturation. Stewart (unpublished bench notes), working with fed and active juvenile largemouth bass held in 12-gal jars at 26 C, found that any reduction in oxygen concentration below air saturation reduced the oxygen consumption rate of bass. Similar results may be found in Fisher's unpublished bench notes, but Fisher worked with fed and active juvenile coho salmon at 20 C. It seems, then, that food consumption, growth, and oxygen consumption rates of bass held in jars can be limited by oxygen concentration at or near the air-saturation level, when food is unrestricted. Therefore, the total metabolic rate, food consumption, and growth of my bass held in aquaria at 20 C and fed to repletion may have been restricted by oxygen. This idea lends strength to the supposition that the oxygen concentration was limiting the total metabolic rate of bass in the ponds, regardless of the food density, although appropriate experiments will have to be conducted to provide final proof.

The results of the temperature experiments reported in this thesis clearly demonstrate that temperature can be an important factor regulating the food consumption and growth of bass. The food consumption and growth rates of bass fed unrestricted rations were observed to be highest at the highest test temperature and lowest at the lowest test temperature for each season of the year. Bennet (1937) compared the growth of Wisconsin largemouth bass with the growth of Louisiana largemouth bass and reported that the southern fish grew more rapidly than those in the northern state. Warmer water temperatures and a longer growing season were believed to explain these observations. Kramer and Smith (1960) found that the growth of largemouth bass is directly correlated with temperature. Strawn (1961) demonstrated that the growth rates of largemouth bass fry in a Minnesota lake were retarded at low water temperatures and accelerated at high water temperatures. Coble (1967) reported that growth of adult smallmouth bass in nature can be related to water temperature, but suggests that other factors may influence total annual growth as much as, or more than, temperature does.

Bass held in aquaria, where food was readily available, were found to consume food and grow at 10 C. In nature, however, where the food supply is often limited, it is likely that bass will not gain weight at temperatures below about 10 C. Markus (1932) reported that largemouth bass did not feed at temperatures below 10 C. Negligible growth of bluegills when the water temperature fell below 10-13 C in fall and spring seem to support these findings (Anderson, 1959).

Results presented in this study suggest that a decrease in temperature causes the food consumption-growth rate curves to flatten out at lower food consumption rates. Anderson (1959) found food assimilation efficiency to decrease with temperature and suggests that this may be due to differences in the effectiveness with which fats are removed from the food in the gut. He found that the fat content of the feces of the bluegill increased as temperature decreased from 26, to 20, to 16, and to 10 C. Assimilation efficiency experiments conducted in this investigation seem to support Anderson's finding, although only a few tests were conducted. The activity of carp digestive enzymes on a specific substrate has been observed to vary depending on the season of the year (Chepik, 1964). Chepik observed that enzyme activity and digestive rate were high in spring and summer and low in winter. Rates of digestion of proteins decreased in winter by 47-66%, those of carbohydrates by 59-67%, and those of fats by 37-70%.

Reduced oxygen concentration has been shown to inhibit food consumption and growth of both bass and coho salmon fed to repletion (Stewart, et al., 1967; Fisher, 1963). As was previously discussed, the total metabolic rate of bass may be limited directly or indirectly by oxygen concentration at or very near the air-saturation level at moderately high temperatures. The metabolic rate of an actively feeding bass is probably controlled by temperature and limited by oxygen concentration, except at low temperatures where oxygen concentration may have little effect on food consumption and growth.

At a high prey density, it seems likely that a reduction in oxygen concentration would lower the total metabolic rate of bass, thus reducing food consumption and growth. Although bass production might be greatly reduced, some growth would probably occur, the bass only growing less rapidly. However, at relatively low prey densities, a reduction in oxygen concentration might have a far greater effect on a bass population, since it might decrease food consumption to a level where growth would not be possible. In nature, the survival of a population of fish would be in question if the individual fish in the population failed to grow for very long periods. Brocksen et al. (1968) concluded that the growth rate of a predator can be closely correlated with prey density when food is a limiting factor, at least in laboratory streams. The results obtained in the pond study reported here essentially substantiate this conclusion, although it appears that the oxygen concentration in the water may also limit the growth rate of predatory fish, particularly at moderately high temperatures.

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APPENDICES

Appendix I. Initial and final weights and lengths, feeding level, and total food consumption for bass held in the laboratory test vessels. All values are based on wet weights and lengths.

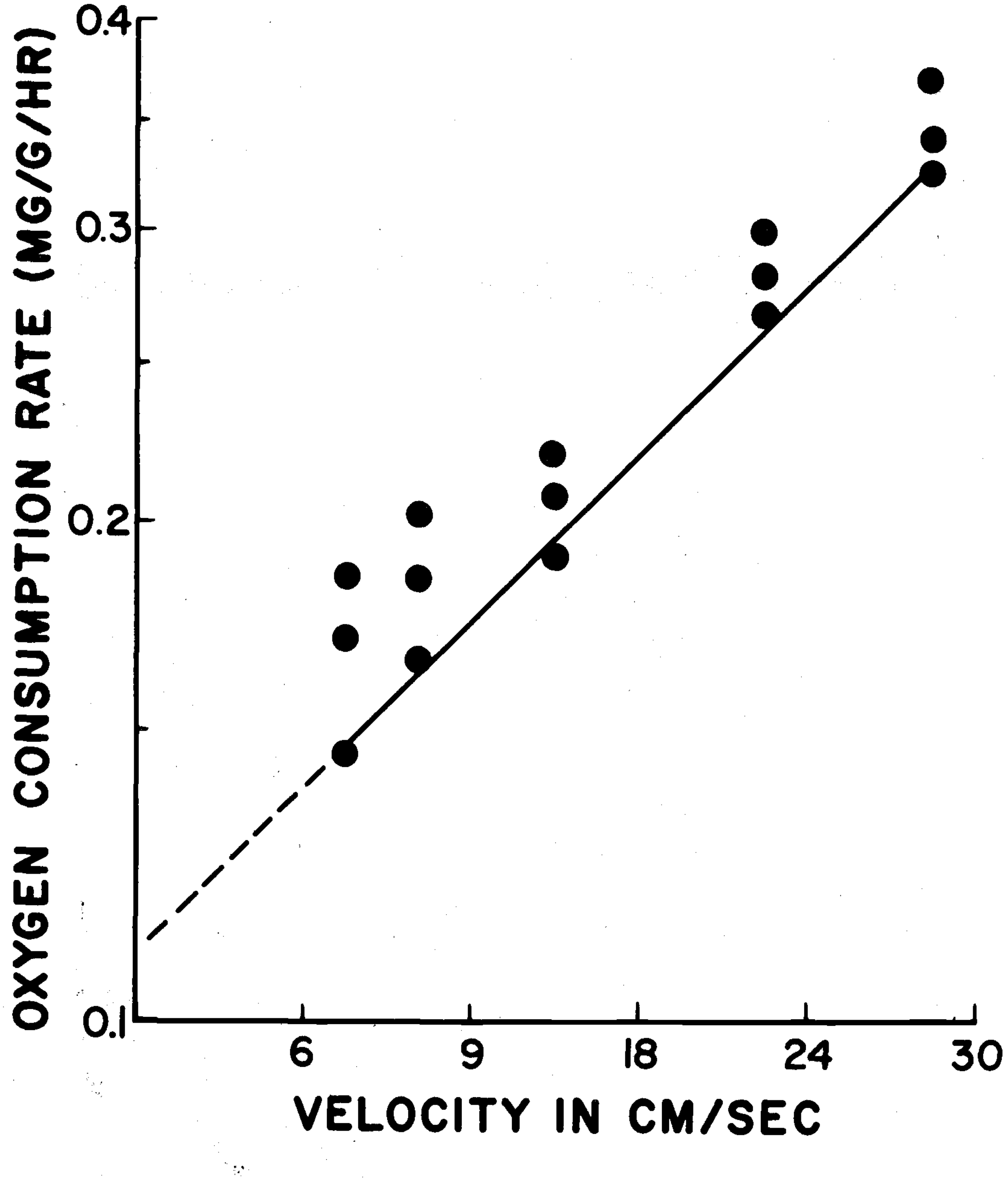
Experiment number	Mean temperature and range (C)	Feeding level	Total food consumed (g)	Weight of bass (g)		Length of bass (cm)	
				Initial	Final	Initial	Final
1	31.0	1-O	-----	4.07	3.62	7.5	7.5
	(30.4-31.8)	2-O	-----	4.08	3.60	7.4	7.4
		1-A	1.00	3.90	4.00	7.2	7.5
		2-A	0.90	4.42	4.49	7.5	7.7
		1-B	4.84	3.80	6.10	7.1	8.3
		2-B	4.75	3.85	6.09	7.2	8.4
		1-C	16.61	3.69	10.64	7.0	9.2
		2-C	16.49	3.91	10.64	7.3	9.2
2	27.5	1-O	-----	5.28	4.76	8.1	8.0
	(21.0-28.5)	2-O	-----	4.78	4.38	7.9	7.9
		1-A	1.12	6.03	6.29	8.4	8.6
		2-A	1.17	5.88	6.19	8.3	8.4
		1-B	5.28	5.40	8.08	8.2	9.0
		2-B	5.14	4.70	7.43	7.8	8.4
		1-C	19.80	5.72	13.98	8.3	9.8
		2-C	20.24	5.94	15.62	8.5	10.1
3	22.9	1-O	-----	4.40	4.12	7.2	7.4
	(22.0-23.2)	2-O	-----	5.15	4.69	7.7	7.7
		1-A	0.95	4.49	4.83	7.5	7.6
		2-A	1.13	5.56	5.96	7.8	8.5
		1-B	4.86	5.63	8.04	7.9	8.8
		2-B	4.93	5.07	7.74	7.6	8.6
		1-C	13.68	6.25	13.29	8.4	9.7
		2-C	14.50	5.92	12.53	8.2	9.3
4	25.1	1-O	-----	46.6	44.1	15.3	15.3
	(24.8-25.3)	1-A	11.49	54.8	59.0	16.5	16.6
		1-B	18.08	43.6	50.7	14.9	15.3
		1-C	23.09	58.8	68.2	16.9	17.6
5	30.0	1-O	-----	56.8	52.7	17.0	16.9
	(29.5-30.5)	1-A	6.52	59.0	58.3	17.6	17.6
		1-B	20.21	58.6	63.9	16.9	17.1
		1-C	31.38	56.5	67.7	17.3	17.7
6	26.0	1-O	-----	6.11	5.47	7.9	7.9
	(25.7-26.2)	1-A	1.14	6.14	6.09	7.9	8.0
		1-B	6.12	6.46	9.10	8.1	9.0
		1-C	13.08	6.00	11.88	7.9	8.7
		2-C	17.00	5.40	12.15	7.7	8.7

Appendix I. (Continued)

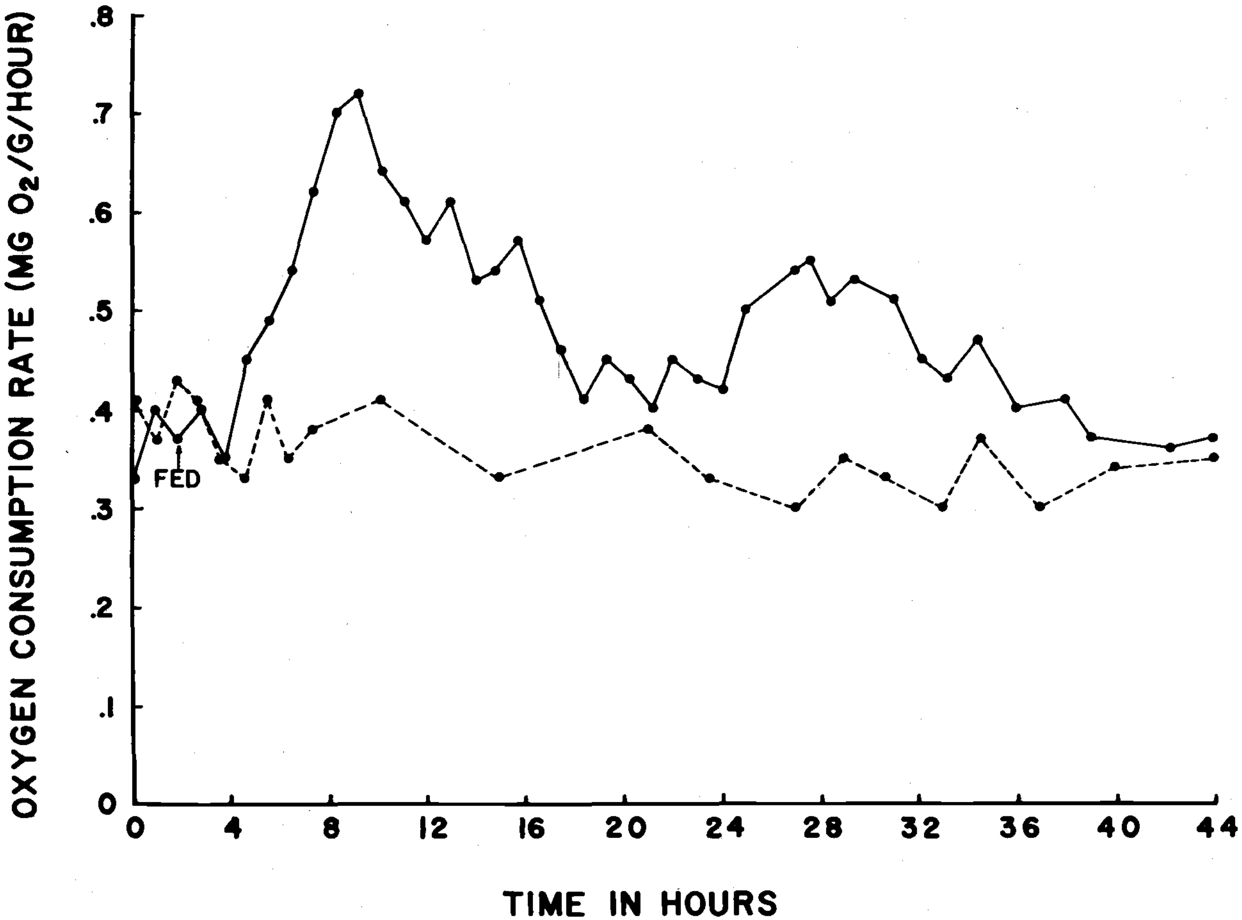
Experiment number	Mean temperature and range (C)	Feeding level	Total food consumed (g)	Weight of bass (g) Initial	Weight of bass (g) Final	Length of bass (cm) Initial	Length of bass (cm) Final
7	20.0	1-O	-----	7.24	6.58	8.5	8.5
	(19.6-20.2)	2-O	-----	9.20	8.60	9.0	9.0
		1-A	1.56	8.34	8.66	8.9	9.0
		2-A	1.25	7.29	7.47	8.6	8.8
		1-B	6.81	8.33	11.07	8.9	9.3
		2-B	6.77	7.35	10.68	8.7	9.5
		1-C	17.43	8.12	14.25	8.8	9.9
		2-C	5.13	7.98	11.82	8.8	9.5
		3-C	8.48	7.05	10.89	8.4	9.4
		4-C	9.01	6.69	10.99	8.2	9.1
8	15.0	1-O	-----	5.75	5.38	8.0	8.0
	(13.4-16.0)	2-O	-----	4.40	4.19	7.4	7.3
		1-A	1.20	5.59	6.10	7.8	8.1
		2-A	1.07	4.66	4.85	7.2	7.4
		1-B	3.86	4.92	5.91	7.6	7.8
		2-B	3.68	5.35	6.58	7.5	7.8
		1-C	4.08	5.01	5.90	7.5	7.8
		2-C	6.47	5.31	6.50	7.3	7.9
9	9.9	1-O	-----	4.10	3.85	7.2	7.2
	(9.2-11.2)	2-O	-----	3.73	3.56	7.0	7.0
		1-A	0.39	4.11	4.12	7.2	7.3
		1-B	0.87	3.76	4.20	7.3	7.4
		2-B	0.44	3.76	3.71	7.0	7.2
		1-C	1.47	4.80	5.08	7.5	7.5
		2-C	1.12	3.50	3.70	7.1	7.1
10	14.9	1-O	-----	3.27	3.24	6.7	6.7
	(14.1-15.5)	2-O	-----	3.68	3.49	6.9	6.9
		1-A	0.68	3.39	3.72	6.8	6.8
		2-A	0.76	3.57	3.82	7.1	7.3
		1-B	1.62	3.24	3.79	6.8	7.0
		2-B	1.53	3.79	4.36	7.2	7.3
		1-C	3.05	3.32	4.16	6.8	7.0
		2-C	3.08	3.52	4.53	6.9	7.2
11	20.2	1-O	-----	4.58	4.26	7.7	7.7
	(19.8-20.6)	2-O	-----	3.90	3.67	7.3	7.2
		1-A	0.92	4.00	4.15	7.5	7.6
		2-A	0.72	4.36	4.50	7.7	7.8
		1-B	2.64	4.28	5.32	7.5	7.7
		2-B	3.02	4.04	5.41	7.4	7.9
		1-C	5.72	4.10	5.85	7.5	7.9
		2-C	4.43	4.14	5.96	7.5	7.9

Appendix I. (Continued)

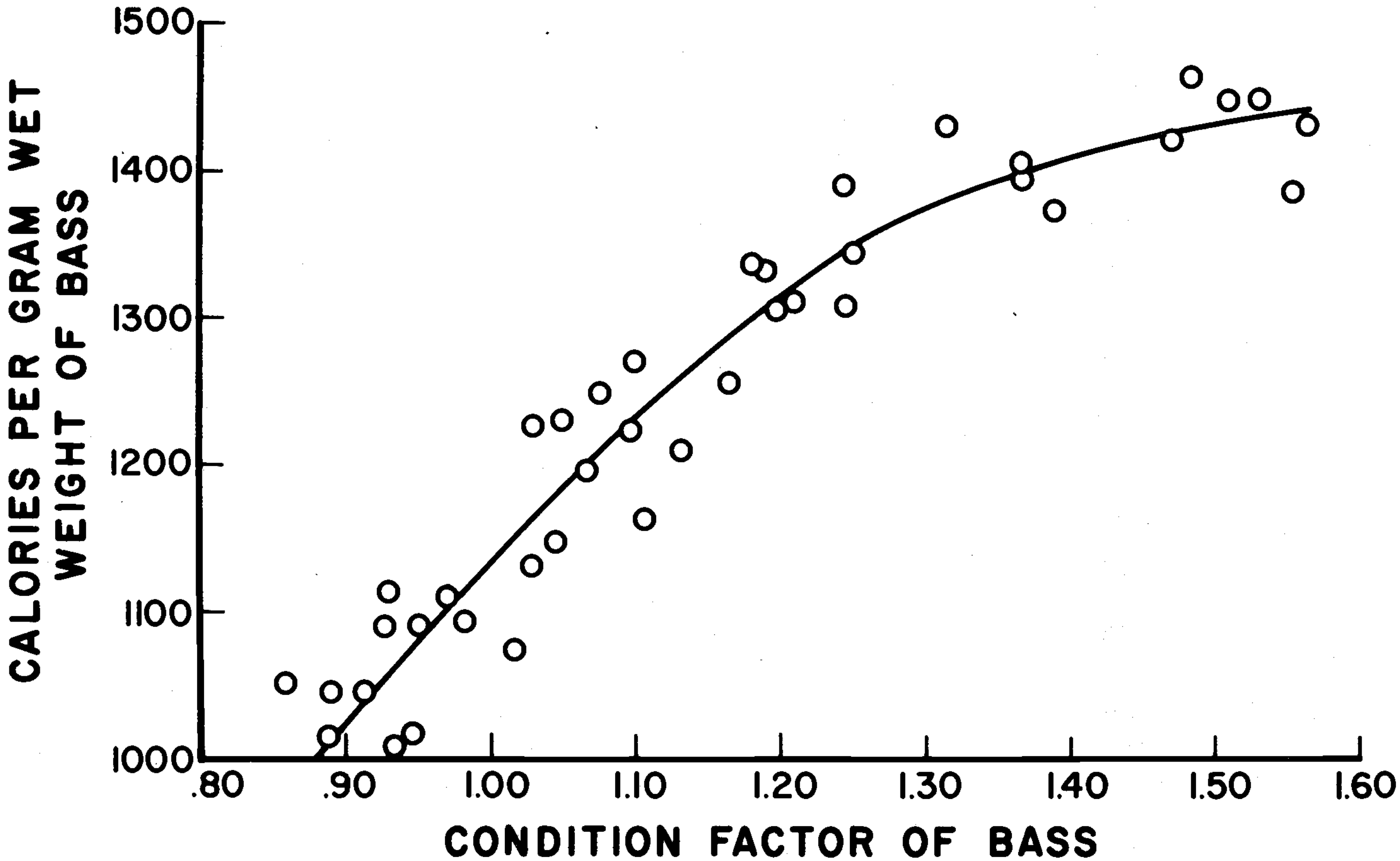
Experiment number	Mean temperature and range (C)	Feeding level	Total food consumed (g)	Weight of bass (g)		Length of bass (cm)	
				Initial	Final	Initial	Final
12	20.0	1-O	-----	5.18	4.90	7.9	7.8
	(19.8-20.0)	2-O	-----	5.14	4.80	7.7	7.7
		1-A	0.86	5.04	5.15	7.5	7.7
		2-A	0.83	5.64	5.73	8.0	7.9
		1-B	3.31	4.98	6.19	7.6	7.9
		2-B	3.57	5.70	6.96	7.8	8.2
		1-C	9.60	5.10	8.18	7.7	8.3
		2-C	9.82	5.13	8.68	7.9	8.4
13	14.8	1-O	-----	5.07	4.79	7.6	7.6
	(14.1-15.2)	2-O	-----	5.19	4.74	7.6	7.6
		1-A	0.72	4.79	4.83	7.3	7.4
		2-A	0.48	5.43	5.22	7.8	7.8
		1-B	2.06	5.61	6.43	7.8	7.9
		2-B	2.30	4.93	5.92	7.5	7.8
		1-C	5.34	5.26	6.74	7.7	8.0
		2-C	5.25	5.34	6.65	7.8	8.0
14	25.3	1-O	-----	5.60	5.08	7.8	7.8
	(24.4-26.0)	2-O	-----	5.47	5.13	7.8	7.7
		1-A	0.95	3.74	3.85	7.0	7.1
		2-A	0.88	4.95	4.99	7.5	7.5
		1-B	3.00	5.81	6.55	8.1	8.2
		2-B	3.38	5.75	6.87	8.2	8.3
		1-C	8.60	4.61	9.54	7.4	9.1
		2-C	9.56	4.50	10.15	7.5	9.3
15	20.0	1-O	-----	6.15	5.90	8.2	8.2
	(19.5-20.3)	2-O	-----	7.91	7.64	8.7	8.7
		1-A	1.30	7.32	7.56	8.5	8.7
		2-A	1.22	7.33	7.41	8.5	8.8
		1-B	3.94	6.63	8.29	8.3	8.9
		2-B	4.07	6.49	8.36	8.3	8.8
		1-C	13.47	7.44	11.85	8.6	9.7
		2-C	14.01	6.91	11.26	8.4	9.2



Appendix II. Oxygen consumption rates of juvenile largemouth bass in relation to water velocities in which the bass were forced to swim at 20 C. The straight line was fitted by eye to the lowest oxygen consumption rate obtained at each activity level.



Appendix III. The relationship between oxygen consumption rate of a juvenile largemouth bass fed one ration of food (mosquitofish) at 20 C and forced to swim at 6.5 cm/sec and time in hours after feeding is illustrated by the solid line. The dashed line depicts the oxygen consumption rate of an unfed bass which has not received food for 54 hours and was forced to swim at 6.5 cm/sec at 20 C.



Appendix IV. The relationship between body condition factor and calories per gram wet weight of juvenile largemouth bass.