

## The growth of largemouth bass, *Micropterus salmoides* (Lacepede), under constant and fluctuating temperatures

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(Received 20 January 1983, Accepted 21 April 1983)

Growth of largemouth bass, *Micropterus salmoides*, was tested under constant (15° C, 29° C) and cyclic (18 h at 15° C, 6 h at 29° C) temperature conditions. Six groups of 10 fish each were tested; one group under each constant condition, and four groups in the thermocycles. The four latter groups differed in the timing of their feeding; one group each was fed at the start and middle of the warm and cool periods, respectively. All groups were fed to near-satiation. The fish fed at the start of the warm cycle and start cool group grew most rapidly, followed by the constant warm, mid warm, mid cool, and constant cool groups. These data were evaluated in relation to vertical migrations of fish to test the physiological enhancements that may be important to vertical migrations. Apparently thermocycles allow more rapid consumption of food than constant cool conditions and lower metabolic rates than constant warm conditions, which allows some fish to grow more rapidly under thermocycles than under constant conditions at either extreme of the cycle. However, the timing of feeding in relation to temperature in the thermocycle is important in the degree of growth enhancement.

### I. INTRODUCTION

Vertical migrations in zooplankton and other limnetic animals are well known, and the adaptive significance of these movements have been attributed to escape from predation (Cushing, 1951), group reproductive behaviour (Wynne-Edwards, 1962; David, 1961), seeking optimum light levels (Harris, 1953), and utilization of thermal stratification to optimize growth (McLaren, 1963). Recently the last argument has been most readily accepted, although components of each of these ideas probably influence the extent and pattern of vertical migration. The physiological significance of diel cycles of body temperature in sockeye salmon, *Oncorhynchus nerka*, have been expounded by Brett (1971), and include (1) the ability to digest more food in warmer water, (2) the ability to consume more food in warm water, due to the rapid digestion rate, and (3) the minimization of maintenance costs by resting in cooler water. Brett hypothesizes that vertical migrations of fish will enhance growth, particularly when food is limiting. Experimental studies by Biette & Geen (1980), Cox & Coutant (1981), and Spigarelli *et al.* (1982) all support the hypothesis of better growth under thermal cycles than under constant temperatures at the mean of that cycle. However, only Biette & Geen (1980) were able to demonstrate more rapid growth under thermal cycles than at the constant warm temperature extreme, and this was only true for fish fed less than satiation ration. The most relevant choice comparison for most fish in the wild is probably either constant cool, constant warm, or a diel cycle; so the test between thermal cycles and the two extreme temperatures is ecologically most meaningful. Also, the relationship between growth and temperature cycles largely depends on the

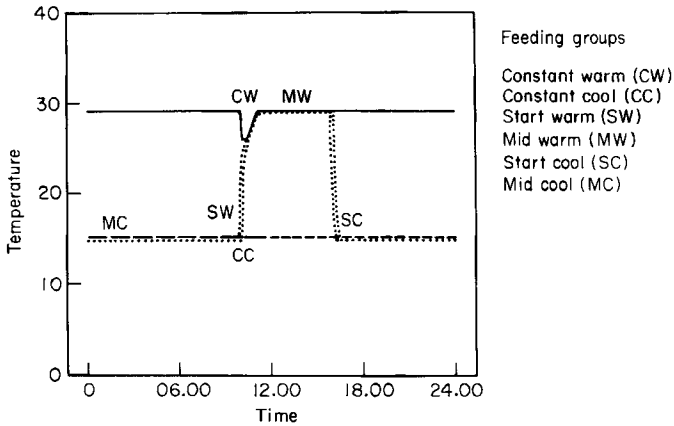


FIG. 1. The diel temperature cycles for fish under constant warm (—), constant cool (---), and diel cycles (...); as well as the timing of feeding for each experimental group.

temperatures tested and the fish's temperature-growth relationship (Hokanson *et al.*, 1977). Cycles of temperatures with means below the optimum temperature for growth generally will enhance growth, while those with means exceeding the optimum will probably depress growth, when compared to growth under a constant temperature at the mean of the cycle (Cox & Coutant, 1981).

If Brett's (1971) energy optimization hypothesis is true, then one should find differences in growth of fish in thermal cycles depending on the time in the cycle when they are fed. One might hypothesize that fish fed during the warming period in a cycle should be able to digest and consume more food than fish fed during the cooling period, due to the more rapid digestion process occurring during feeding at warmer temperatures. Routine metabolic rate should be similar between these different groups (Diana, 1983), while the relationship between thermal cycles, feeding, and apparent specific dynamic action is largely unknown.

The purpose of this study is to evaluate the relationship between cyclic thermal regimes, timing of feeding, and growth of largemouth bass, *Micropterus salmoides*. In particular, data are collected to test the extrapolation of Brett's hypothesis on the physiological mechanisms involved in the optimization of growth by fish in thermal cycles.

## II. MATERIALS AND METHODS

The diel temperature cycle chosen for this study was 18 h at 29°C and 6 h at 15°C. The cycle is nearly the same as used in Diana (1983), with a slight expansion of the warm cycle to permit feeding a group of fish in the middle of the warm period. The maximum and minimum temperatures represent the largest voluntary change in body temperature that largemouth bass could experience in most Michigan lakes (Diana, 1983).

Largemouth bass fry (mean weight 1.2 g) were collected by seine from ponds at the Saline Fisheries Research Area, operated by the Michigan Department of Natural Resources. The fish were held in two groups for 1 week at 15°C, then were randomly sorted into groups of 10 fish each. Six groups represented different feeding times or thermal regimes, while one group was sacrificed to serve as indicators of initial body composition for all fish. Each individual was weighed to 0.001 g, then put into one of the experimental groups.

Three thermal regimes were maintained in six 12-l experimental tanks with flow through water at 0.51 min<sup>-1</sup>. One tank was kept with a constant temperature of 15°C, one with constant 29°C and four with 6 h at 29°C and 18 h at 15°C (Fig. 1). The thermal regimes

were maintained by pumping water from holding tanks at either temperature; thus the cycling tanks had brief periods at the beginning of each new temperature cycle when tank temperature changed rapidly. Tank warming occurred over approximately 1 h, while cooling occurred rapidly over 25 min. The warm water system recycled all water; thus when the warming cycle began in the fluctuating tanks, cool water was mixed into the warm water bath and resulted in a slight lowering of the constant warm tank from 29 to 26°C for approximately 1 h (Fig. 1).

The fluctuating thermal regimes began warming at 10.00 and began cooling at 16.00 hours. Rations were calculated to feed the fish as much as they would willingly consume in about 1 h. The two constant temperature groups and one cycling group (start warm) were fed at 10.00 hours, then the remaining three cycling temperature groups were fed at 13.00 (mid warm), 16.00 (start cool), and 01.00 hours (mid cool), respectively. These four feeding times represented fish which fed at the beginning or middle of the warm or cool cycle (Fig. 1). Rations were initially set at 72% of satiation by weight (calculated from model in Rice *et al.*, 1983 based on data from Niimi & Beamish, 1974) for all groups; satiation ration of fish under fluctuating temperatures was assumed to be the same as for fish under constant warm conditions. Actual feeding rates could not be monitored, as some remaining food was washed out of the tanks if it was not quickly eaten. The ration was adjusted over the first week to achieve a maximum rate of consumption (with no excess left) over 1 h, and then was adjusted weekly to account for growth of the fish (Table I). Average feeding rate of the warm test groups was 83% satiation (by weight); while the constant cool test group was fed in excess of satiation (107%).

All fish were fed previously frozen bloodworms. The food was thawed, strained in a net to remove excess water, then weighed into pans to achieve the group ration level and refrozen in the pans. The food was thawed prior to feeding. At 10.00 each day, the constant warm, constant cool, and start warm groups were fed; the remaining groups were fed by automatic feeders which were loaded at 10.00. Prior to feeding, all faeces and any remaining food were siphoned from each test tank.

Weights of individual fish were measured at the start of the experiment. The constant warm, constant cool, and start warm groups were weighed weekly to calculate ration adjustment for all groups. After 15 days, all fish were weighed and five fish from each group were sacrificed for water and caloric determinations. The remaining fish in each group were returned to their tanks and held for 15 more days under similar conditions, then sacrificed.

At the termination of the experiments, each fish was weighed to 0.001 g, dried at 60°C to constant weight, then reweighed. Dried carcasses were pulverized in a coffee grinder and stored in vials at -25°C for calorific analysis. Calorific equivalents were determined using a Phillipson microbomb calorimeter (Paine, 1971).

The beginning energy content for each fish was estimated using the starting wet weights determined for each fish and multiplying these values by the mean proportion dry matter and calorific equivalent for the initially sacrificed fish. Final energy content was considered the product of the final wet weight, proportion of dry matter, and calorific equivalent determined for each fish. Total growth was calculated as the difference between final and beginning energy contents, and daily growth rate was the total growth divided by the number of days.

Differences between experimental groups were evaluated using analysis of variance and the Least Significant Difference test; they were considered significant if  $\alpha < 0.05$ . Significant differences for one group between times were evaluated using a *t*-test ( $P \leq 0.05$ ).

### III. RESULTS

Virtually all individual fish showed positive growth, and each group showed a significant increase in energy content during the experiment (*t*-test,  $P < 0.05$ ) (Table II). There was no significant differences in the daily growth rate of fish fed for 15 or 30 days, except for the start cool group (Table II). In that group, some problem occurred during the last week of the experiment, and the fish ceased

TABLE I. Weight, predicted satiation ration, and actual ration fed each group of bass during various periods of the study. Satiation ration = g day<sup>-1</sup>, percentage body weight per day in parentheses. Actual ration = g (or Kcal) day<sup>-1</sup>, percentage of predicted satiation ration in parentheses. Assumption for predicted satiation ration: 1 kcal = 1 g

Group	Date	Mean wet weight	Predicted satiation ration	Actual ration	
				g day <sup>-1</sup>	kcal day <sup>-1</sup>
Constant warm	Aug. 5	1.15	0.336(29)	0.25(74)	0.20(58)
	Aug. 13	1.18	0.342(29)	0.30(88)	0.23(68)
	Aug. 20	1.38	0.380(28)	0.32(84)	0.25(66)
	Aug. 27	1.46	0.394(27)	0.40(102)	0.31(79)
Constant cool	Aug. 5	1.10	0.130(12)	0.15(115)	0.12(90)
	Aug. 13	1.15	0.134(12)	0.15(112)	0.12(87)
	Aug. 20	1.33	0.148(11)	0.15(101)	0.12(79)
	Aug. 27	1.34	0.149(11)	0.15(101)	0.12(79)
Start warm	Aug. 5	1.17	0.340(29)	0.25(74)	0.20(57)
	Aug. 13	1.27	0.360(28)	0.30(83)	0.23(65)
	Aug. 20	1.50	0.402(27)	0.32(80)	0.25(62)
	Aug. 27	1.75	0.447(26)	0.40(89)	0.31(70)
Mid warm	Aug. 5	1.17	0.340(29)	0.25(74)	0.20(57)
	Aug. 13	—	—	0.30	0.23
	Aug. 20	1.49	0.401(27)	0.32(80)	0.25(62)
	Aug. 27	—	—	0.40	0.31
Start cool	Aug. 5	1.33	0.371(28)	0.25(67)	0.20(53)
	Aug. 13	—	—	0.30	0.23
	Aug. 20	3.94	0.294(31)	0.32(109)	0.25(85)
	Aug. 27	—	—	0.40	0.31
Mid cool	Aug. 5	1.09	0.324(30)	0.25(77)	0.20(60)
	Aug. 13	—	—	0.30	0.23
	Aug. 20	1.27	0.360(28)	0.32(89)	0.25(69)
	Aug. 27	—	—	0.40	0.31

feeding. The growth rate for this group over the last 15 days of the experiment therefore declined, and those four fish will be excluded from further analysis. In addition, there were no significant differences in calorific equivalents or percentage dry matter between any of the experimental groups, between initial controls and final values, or between fish run 15 or 30 days (Table III).

The daily growth rate of fish in each group (Fig. 2) varied in response to thermal regime and feeding group (analysis of variance,  $P < 0.05$ ). The most rapid growth occurred for fish under the thermal cycles which were fed at the beginning of the warming or cooling cycle; these fish had significantly higher growth rates than the fish held at constant 15°C or fish fed in the middle of the cool period. The other groups of fish exhibited growth rates which were statistically similar ( $P > 0.05$ , Least Significant Difference test).

The feeding level for each group approximated satiation in g day<sup>-1</sup>. However, the caloric content (5.5 kcal g<sup>-1</sup>) and relative of dry matter (14.2%) in the food was low, resulting in a lower level of caloric intake (a mean of 65.1% of satiation,

TABLE II. The growth rate of fish under each experimental condition after 15 and 30 days duration

Group	Time (days)	Growth (cal day <sup>-1</sup> )	
		Mean	S.E.
Constant warm	15	40.8	12.5
	30	38.5	7.5
Constant cool	15	23.6	3.4
	30	20.5	4.6
Start warm	15	46.3	8.6
	30	42.3	7.9
Mid warm	15	38.5	4.4
	30	33.1	6.9
Start cool	15	58.8*	24.4
	30	10.5*	5.4
Mid cool	15	23.4	8.0
	30	24.3	2.4

\*Significantly different from each other, *t*-test,  $P < 0.05$ .

TABLE III. Calorific equivalents (kcal g<sup>-1</sup> dry weight) and percentage dry matter for fish from each group, and for fish tested after 15 or 30 days of holding,  $\bar{x} \pm$  S.D.

Group	No.	Calorific equivalent	Percentage dry matter
Constant warm	10	4.9 ± 0.2	23.4 ± 1.5
Constant cool	10	5.0 ± 0.2	22.3 ± 0.8
Start warm	10	5.1 ± 0.3	24.3 ± 1.7
Mid warm	10	5.0 ± 0.1	24.2 ± 1.9
Start cool	9	4.9 ± 0.3	22.5 ± 2.8
Mid cool	9	4.8 ± 0.3	22.9 ± 2.0
Initial controls	5	4.9 ± 0.1	19.9 ± 0.7
Grouped means			
- 15 days	30	4.9 ± 0.2	22.6 ± 1.6
- 30 days	28	4.9 ± 0.3	24.1 ± 2.0

Table I). The fish in each group would not willingly eat more than the allotted ration in an hour, indicating some degree of satiation; but the energetic value of this ration was much less than for food with higher caloric density.

#### IV. DISCUSSION

The thermal cycles and feeding regimes tested in this experiment allowed two groups of fish to grow significantly better than fish fed under constant cool or in the mid cool cycle. Large but statistically insignificant differences in growth

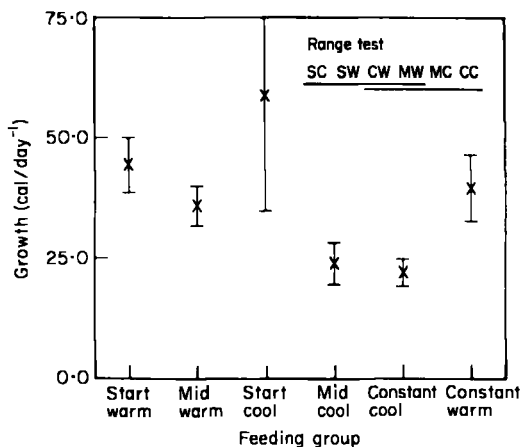


FIG. 2. Growth rates of fish under the various feeding and thermal regimes.  $\bar{x} \pm$  s.e. Range test = Least Significant Difference test, groups underlined at the same level are not significantly different ( $P > 0.05$ ).

occurred among most of the groups; and a ranking of growth (highest to lowest) would be start cool, start warm, constant warm, mid warm, mid cool, and constant cool. This ranking agrees somewhat with Brett's (1971) hypothesis that feeding during the warm portion of the cycle would enhance digestion and increase ration, since the groups fed during the warm cycle grew more rapidly than those fed during the cool cycle (means = 40.1 v. 35.5 cal day<sup>-1</sup>). However, the minimization of metabolic rate during the cool cycle did not always occur as predicted by the energy optimization hypothesis, since only two groups of fish in thermocycles grew more rapidly than the constant warm group. Some problems in extrapolation occurred, however, since the start cool group had the highest growth rate of all. This group exhibited reduced growth during the second 15-day period, resulting in exclusion of those data, and the initial 15-day results were unreplicated. If the mean 30-day value is used (34.7 cal day<sup>-1</sup>), the results fall much better into line as predicted.

Problems deriving significant differences in growth rates between the groups influenced the general applicability of this study. At least two major factors influence the variability in growth within a group: group size and fish size. Sizes of fish in each group were as similar as possible at the start of the experiments. The growth of individual fish may be significantly altered when the fish are tested in a group; both enhanced growth (Brett, 1979) and reduced growth (Brown, 1957) have been demonstrated, and are believed to occur in response to different social interactions. Young largemouth bass are schooling fish (Elliott, 1976), and thus I felt that holding fish in groups would not reduce individual growth. There were no significant differences in growth for fish held 15 or 30 days, when group size was reduced by half, indicating that group size did not largely alter average growth. In addition, there were no major changes in the standard error of the growth rate between these two time periods (when density was reduced by half), indicating that group size did not affect the variability of individual growth rates. Bass and other top piscivores are notorious for the daily variability in their feeding and growth rates (Smagula & Adelman, 1982; Diana, 1979), and this factor undoubtedly affected the total amount of variation found.

For this study, fish were taken from holding conditions at 15° C and put under cyclic or constant warm conditions. Thus, any initial stress or acclimation responses would affect the final growth rate. Since growth rate did not differ substantially between the 15 and 30 day trial groups, the lack of preconditioning to temperature probably did not alter growth rate. The rate of temperature acclimation in bass is very rapid (Venables *et al.*, 1977), and they also exhibit no metabolic stress when tested under thermal cycles similar to the present study (Diana, 1983). These results indicate that largemouth bass are apparently very robust in their reaction to rapid temperature change.

Brett (1971) hypothesized that vertical migrations in sockeye salmon were energetic responses to optimize growth under limited rations, and these ideas were supported by Biette & Geen (1980). The present study was designed to test growth under maximum ration, but ration was reduced slightly to ensure consumption of food over limited time periods (1 h). Unfortunately, the rations were set by weight of the food; when caloric density was accounted for, they only equalled 65% of satiation. Thus, these results are similar in respect to Bietta & Geen (1980). Since higher ration levels were not tested, the ability to extrapolate these results to other ration levels is uncertain.

The results of this study and Diana (1983) allow prediction of some consequences of vertical migrations for largemouth bass in the field. The general pattern of vertical migrations in fish is probably related to patchy availability of thermal and food resources. For example, if food is available at all depths and temperatures, then fish should utilize constant temperatures near the optimum for growth (Brett, 1971). If food is limited to temperatures above the optimum, then vertical migration to feed at warm temperatures and rest at cool temperatures might allow a more rapid growth rate than constant warm temperature occupation (Magnusson & Crowder, 1981). If food is only available at temperatures below optimum for growth, it is uncertain if diel cycles of temperature would allow more rapid growth than constant cool water occupation. Data from this study suggest that there would be no advantage to vertical migration under these latter conditions.

Financial support for this study was provided by the School of Natural Resources, University of Michigan. Dr Paul Webb and Mr Chris Johnsrude provided logistic support. Mr Percy Laarman and the Michigan Department of Natural Resources supplied the fish. James Rice aided in interpreting the ration model. Contribution number 373 of the Great Lakes Research Division, University of Michigan.

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