

Effects of Temperature Acclimation on the Swimming Ability of Smallmouth Bass Fry

R. WELDON LARIMORE AND MICHAEL J. DUEVER¹
Illinois Natural History Survey, Urbana, Illinois

ABSTRACT

Entire year classes of smallmouth bass are frequently lost in midwestern streams during floods that occur when the fry are less than 25 mm long. Since changes in air and water temperatures often accompany these floods, the effects of temperature on swimming ability of fry 20–25 mm in length were measured in the laboratory and related to floodwater conditions. Groups of fry were acclimated to temperatures of 5, 10, 15, 20, 25, 30, and 35 C and tested for swimming ability at each of these temperatures. The maximum swimming speed for fish acclimated to a particular temperature increased with successively higher test temperatures, to a level above which swimming ability declined rapidly. Swimming speeds attained were progressively higher for each higher level of acclimation with the exception of those from the upper extreme of 35 C. The best swimming performance was at a temperature above the acclimation temperature for all fry except those acclimated to 30 and 35 C and these fry failed to swim above their acclimation temperatures. Temperature changes in streams may not directly cause the displacement of smallmouth bass fry but may reduce their swimming ability and thereby contribute to their displacement when exposed to turbid and turbulent floodwaters.

INTRODUCTION

Reproduction of smallmouth bass, *Micropterus dolomieu* Lacépède, in warmwater streams is often interrupted by extreme weather changes which occur commonly during the late spring and early summer. These weather changes are frequently accompanied by violent fluctuations in stream flow, temperature, and turbidity.

In Illinois, a period of 3 to 4 weeks is required from nesting and egg laying until the young bass are past the black-fry stage (more than 25 mm long) and able to withstand relatively severe environmental changes. The overall nesting season for the smallmouth bass in this area generally extends from the middle of May through June, permitting time for several nesting attempts.

Intensive observations of bass reproduction have been made on three small, warmwater streams in Vermilion County, east-central Illinois. From 1950 through 1958, reproduction was successful during four of the nine breeding seasons. Although young were observed at one time or another in all years, they disappeared in years when periods of flooding occurred while the fry were still in the black-fry stage. Fish collections taken after these floods indicated that these year classes of smallmouth bass had been destroyed.

Frequent failure of smallmouth bass to establish year classes in years of flooding drew our attention to the various conditions which may influence reproduction. The loss of nests, eggs, or fry has been associated with temperature change, siltation, strong currents, and other factors accompanying stream flooding. Cleary (1956) reviewed these relationships. The specific influences have not been certain. The small black fry (fry up to 25 mm) after leaving the nest are able to swim vigorously and feed on a variety of foods. The reason for their disappearance during the floods was not understood.

In an attempt to distinguish factors that contribute to reproductive failure, we initiated a laboratory study in which the effects of various factors, namely temperature, turbidity, turbulence, and water velocity, could be separated. Initially, it was believed that a single environmental factor might be responsible for fry destruction; for example, the sudden increase in turbidity, usually associated with floods, might either inhibit feeding or disturb the orientation of the fry, causing them to lose their position in flowing water. Although evidence now indicates that destruction of reproductive products results from a complex relationship between several factors, it was expedient to first consider the effects of each factor separately.

This paper deals primarily with thermal

¹ Present address: Department of Zoology, University of Georgia, Athens, Georgia.

conditioning and its influence on the swimming ability of smallmouth bass fry. The objective was not to determine maximum swimming speeds or endurance, or to make energy measurements, but simply to measure the displacement of fry with different thermal histories, when exposed to various water velocities and temperatures. We felt that displacement from their place of orientation in the stream was the important effect that might be caused by flood waters.

SOURCE AND CONDITIONING OF FISH

The smallmouth bass used in this experiment were in the black-fry stage, between 20 and 25 mm total length with a mean length of 22 mm.

All experimental fish were collected from two deep gravel pits in Ford County, Illinois. Although produced by stocks that had been taken from an Illinois stream several years earlier, these fry developed under conditions somewhat different from those for stream fry. Fry from the gravel pits, however, seemed more suitable for these studies than those from streams because (1) they were of more uniform size, (2) they were from waters with rather stable temperatures and a comparatively uniform thermal history, and (3) they were from an ample available supply not likely to be eliminated by flood waters. These fry had not been exposed to water currents and as test animals they might have been less active than stream-reared fry. Brett, et al. (1958), Hammond and Hickman (1966), and MacLeod (1967) observed substantial increases in swimming performance after their experimental fish had had periods of exercise. Although our test fish were sedentary during the period of thermal acclimation in the laboratory, they had been "normally" active in their lake environment, perhaps to about the same extent as bass fry in central Illinois streams where they seek quiet waters or waters of only moderate velocities.

In experiments involving temperature relationships, it has often been desirable to raise the experimental fish under carefully regulated conditions. Smallmouth bass, however, are difficult to rear in the laboratory; therefore, it was considered expedient to use healthy

and vigorous fry from the gravel pits even though their thermal history was not precisely known and could not be measured for fry that change their positions in a fluctuating habitat.

Fry of approximately 18 mm total length were brought into the laboratory, separated into 7 groups of 20 and placed in water at temperatures of 5, 10, 15, 20, 25, 30, and 35 C. The fish were held at these temperatures for five or more days (longer periods at lower temperatures) before being used as experimental animals. Whether or not a five-day period fully acclimated these fish to the various temperatures is unknown, but a much longer period was impractical, especially at the higher temperatures because the fry would have grown out of the size range required for the experiments.

During the acclimation period, the fry were fed newly hatched lake chubsuckers, *Erimyzon sucetta* (Lacépède), and white worms, *Enchytraeidae*. They fed readily on these items and remained active and apparently healthy. Mortality was very low and thus there was no significant amount of differential survival.

The seven temperature levels mentioned above (5–35 C at 5-degree intervals) were attained in temperature control rooms held at 5, 15, 25, and 30 C. The 10, 20, and 35 C levels were maintained with thermoregulators in rooms at the next lower temperature, for example, 20 C in the 15 C room. Although the air temperature in these rooms fluctuated ± 1 C and varied in different parts of the room, the water in our aquaria varied less than ± 0.5 C. A daily cycle of 12 hours light and 12 hours dark was maintained in each room.

EQUIPMENT AND PROCEDURE

An annular tank, such as used by Fry (1948) and others, was employed in this part of the investigation. It was made of lucite, 16 inches in diameter with a 6-inch-diameter central core, and mounted on a turntable. The turntable speed was controlled by a rheostat (Variac). Revolutions of the turntable were counted visually or with a tachometer and timer clock. The entire assemblage was set up on a laboratory cart that could be moved

easily from one room (one temperature) to another.

Previous investigations of swimming in annular tanks were based on orienting the fish to a fixed sign outside. The small fry, however, would not consistently orient to stationary marks, patterns, shadows, or points of light outside the revolving drum. They did orient to a point of light when the room was in near total darkness, but under these conditions reliable observations were difficult.

We discovered that the fry exhibited an aversion for a bright light above the tank and would readily enter an open-ended cylindrical chamber to avoid it.

A procedure that worked well was to have the fry orient to subdued light by remaining within a small cylindrical chamber suspended in the annular tank (Figure 1). This chamber consisted of a piece of thin-walled steel tube, 1½ inches inside diameter, bent to parallel the arc of the tank at a distance of 2½ inches from the outer wall. The dimensions were 3 inches on the inside curve and 3½ inches on the outside curve with the ends of the tube cut to follow the radii of the annular tank. The forward edge of the tube was sharply beveled. The tube was suspended ½ inch above the bottom and illuminated from above by an incandescent light. The fry would swim vigorously against a current to remain in the tube and avoid the bright light of the open tank.

The testing procedure was as follows:

1. An entire group of 20 acclimated fry was moved to the room in which tests were to be conducted. The water temperature was changed from acclimation temperature to test temperature at the rate of 5 degrees C/15 minutes. The fry showed no reaction to this rate of change.

2. With the annular tank set up, as described above, with well-aerated water adjusted to the selected test temperature and rotating at a slow speed (15 mm/second), a single bass fry was introduced into the rear of the tubular chamber. The fry immediately entered the chamber where the light was subdued. At higher temperatures, when fry were required to swim faster, the tests were begun at progressively greater speeds (up to 80 mm/



FIGURE 1.—Apparatus used to test the swimming ability of smallmouth bass fry.

second at the high temperatures) so that the total experimental period was roughly the same.

3. The initial speed was continued for three minutes. During the third minute, the revolutions per minute were counted. The speed of rotations was slowly increased during the fourth minute to elevate swimming velocity approximately 1 body length or 22 mm/second above the previous speed. This speed was maintained through the fifth minute and counted during the sixth. After the sixth minute, the revolutions were again increased and later counted. Thus, speeds were increased at intervals of 3 minutes, i.e., during the fourth, seventh, tenth, etc. minutes; revolutions were counted during the third, sixth, ninth, etc. minutes.

4. The three-minute sequence was continued through higher speeds until the fry did not or could not remain in the chamber. The fry was reintroduced into the test chamber. If the fry again left the chamber during the following three minutes, this speed was con-

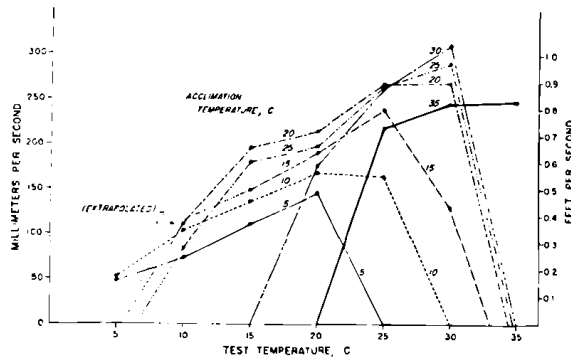


FIGURE 2.—Swimming speeds at which smallmouth bass fry were displaced at various temperatures after acclimation to 5 to 35 C.

sidered the “end point” of the test. If it remained in the chamber, the three-minute sequence was continued.

5. Usually 10 fry from each acclimation temperature were run at each test temperature.

The water mass in the rotating annular tank did not move at the same velocity as the tank itself. Fry and Hart (1948) found that the water and tank moved at a constant ratio of 0.582 : 1 and that the ratio was independent of temperature. Brett, Hollands, and Alderdice (1958) recognized the slippage and simply measured the velocity of water by counting the rotations of a floating marker.

Slippage of the water mass was greatest during periods of acceleration. Since our measurements of swimming speeds were recorded during the third minute after acceleration of the chamber, it was obviously necessary to correct our counts of chamber rotations to equal the actual rotation of the water mass. Water and chamber rotations, during the third minute in our sequence of acceleration, increased in nearly a straight-line relationship throughout the rotation speeds experimentally employed. The estimating equation showed that water rotations = $-0.9280 + 1.0247$ tank rotations.

The relationship of water to tank rotations was based on counts made at approximately 25 C, and we ignored the relatively slight influence of the different temperatures.

The suspended cylinder in which the fry swam during the testing period presented both advantages and disadvantages in swimming

measurements. It gave the fish seclusion, reduced the effects of outside disturbances, and eliminated the need to probe or shock the fish to make it swim. It greatly reduced the error caused by having the fish change position in the tank relative to the center and thus change the path and distance of swimming. This problem was not fully overcome, however, for the velocity gradient from the axis of the annular tank to its outer wall existed through the test cylinder. Fish could still move through 1½ inches (diameter of the test cylinder) of this gradient. Because of this gradient, fish would occupy somewhat lower velocities while swimming in that portion of the cylinder nearest the axis of the annular tank than in the portion toward the outer wall. This difference, expressed as a per cent of the center velocity, would be 13½% less near the inner wall of the cylinder and 13½% greater toward the outer wall. We did not want to restrict the fish to narrower limits in order to reduce these differences. Since the fish did not occupy any consistent position in the test cylinder, the different speeds across the gradient probably averaged a rate near that which was measured for the center.

We were not faced with the even more difficult problem of relating the fish swimming position to the velocity gradient that becomes established from outer wall to center of a long tube, such as has been used and discussed by Ryland (1963). In such a tube with non-turbulent flow, the velocity in the center would be 10 times the velocity near the outer wall. In turbulent flows the relationship between water flow, position of fish, and actual swimming speed would be even more difficult to interpret. Since the length of our test cylinder was only 2 times its diameter and 50 to 300 diameter lengths are necessary for establishment of fully developed turbulent or non-turbulent flow patterns (Rouse, 1946), the gradient of the annular tank was not greatly disturbed by the movement of our suspended test cylinder through it.

Frictional drag on both the inner and outer surfaces of the test cylinder disturbed the flow gradient and increased the opportunity for tactile orientation of the fry. From observations of particles suspended in the flow around

TABLE 1.—Swimming speed in millimeters per second (mean, standard deviation, and coefficient of variation) of fish acclimated to seven temperatures and tested at each of these temperatures

Acclimation temperature, C	Test temperature, C	Number of Fish	Mean total length (mm)	Displacement speed, mm per second			Speed in lengths per second
				Mean	Standard deviation	Coefficient of variation	
5	5	10	22.1	47.9	5.7	11.9	2.2
	10	10	22.1	73.4	9.8	13.3	3.3
	15	15	22.3	111.1	11.7	10.5	5.0
	20	10	22.5	146.1	17.3	11.8	6.5
10	5	10	22.7	52.4	6.8	13.0	2.3
	10	11	22.1	103.4	11.0	10.7	4.7
	15	10	22.7	136.6	14.0	10.2	6.0
	20	11	21.5	167.8	10.8	6.4	7.8
	25	11	21.5	164.8	22.9	13.9	7.7
15	10	8	21.6	71.9*	14.8	20.5	3.3
	15	10	22.0	149.8	15.4	10.3	6.8
	20	10	22.3	190.3	32.6	17.1	8.5
	25	10	23.6	239.0	23.4	9.8	10.1
	30	13	21.9	130.3	30.8	23.6	7.0
20	10	9	21.6	110.8	18.3	16.5	5.1
	15	10	21.9	197.0	18.4	9.3	9.0
	20	10	21.0	215.0	20.7	9.6	10.2
	25	10	21.9	268.2	12.4	4.6	12.2
	30	12	21.8	269.8	34.2	12.7	12.4
25	10	10	23.2	84.6	14.8	17.5	3.6
	15	10	22.4	181.3	16.2	8.9	8.1
	20	10	22.2	198.5	17.8	9.0	8.9
	25	9	22.5	268.2	16.9	6.3	11.8
	30	6	22.5	292.2	23.4	8.0	13.0
30	20	10	22.7	176.8	17.3	9.8	7.8
	25	10	22.7	265.2	11.4	4.3	11.7
	30	10	23.0	311.7	19.5	6.2	13.6
35	25	10	21.8	218.8	35.8	16.3	10.0
	30	10	21.5	247.3	21.3	8.6	11.5
	35	10	21.6	248.8	23.1	9.3	11.5

* This value does not agree with other data (see Figure 2 and text).

the cylinder, we concluded that the frictional drag was minimal and that there was little turbulence in and around the suspended test cylinder. The tactile response of the fry to the inside walls of the cylinder was not believed to be influential except at very low speeds, for the fry swam actively without hugging the wall. At very low speeds, however, the fry did tend to hold near the wall and in light contact with it. Only at the lowest (5 C) temperature, when swimming was most limited, did the contact involve a final determination of performance.

RESULTS

The combined results from all experiments revealed that swimming generally improved after progressively higher levels of acclimation and at progressively higher test temperatures (Figure 2). Fry exposed to each of the combinations of acclimation and test temperature had specific temperatures above and below which they did not swim.

The maximum swimming speed for fish

acclimated to a particular temperature increased with successively higher test temperatures, up to a certain temperature above which swimming ability declined rapidly (Table 1). The positive relationship between increasing test temperatures and improved performance was true for all levels of acclimation although the relationship was somewhat different for fish acclimated to low temperatures and to high temperatures. For fish acclimated to 5, 10, or 15 C, performance improved more gradually and to a lesser total extent above their minimum swimming temperature than it did for those acclimated to 20, 25, 30, 35 C (Figure 2). Also, the decline in performance above the temperature of maximum swimming was less abrupt in the cold-acclimated fish than in the warm-acclimated ones. In fact, fry acclimated to the four higher temperatures failed to swim at any test temperature above that of their best performance.

Swimming speeds attained were progressively higher for each higher level of acclimation, except that those acclimated to 35 C (the

TABLE 2.—*Temperature extremes to which the groups of Smallmouth Bass fry given in Table 1 swam after acclimation to various temperatures*

Acclimation temperature, C	Performance temperature C			
	Minimum	Maximum	Range	Optimum
5	5	20	15	20
10	5	25	20	(23)*
15	10	30	20	25
20	10	30	20	(28)*
25	10	30	20	30
30	20	30	10	30
35	25	35	10	(33)*

* Interpolated from empirical data.

highest acclimation temperature) showed a maximum speed and a peak performance lower than that of fish acclimated to 20, 25, and 30 C. Fry acclimated to 30 C attained a maximum swimming speed somewhat greater than twice that of fry acclimated to 5 C. The difference of only 10 degrees in acclimation temperatures from 10 to 20 C permitted fry to swim approximately 60% faster. On the other hand, a 10-degree difference in acclimation temperature from 20 to 30 C made less than a 20% improvement in swimming.

The best swimming performance was at a test temperature above the acclimation temperature for all fish except those acclimated to 30 and 35 C that failed to swim above their acclimation temperatures. The fastest swimming recorded was for fish acclimated to 30 C and tested at this temperature.

Although the optimum performance temperature was progressively higher for fish acclimated to progressively high temperatures, the range of performance temperatures did not show this progression (Table 2). Fish acclimated to 5 C performed at temperatures of 5 to 20 C, a range of 15 degrees. Fish conditioned to 10 to 25 C performed through a range of 20 degrees. Fish conditioned to 30 to 35 C performed only through a range of 10 degrees.

Only fish acclimated to 5 and 10 C (a range of 5 degrees) performed at 5 C (Figure 2). At the other extreme, only fish conditioned to 35 C performed at 35 C. Fish from acclimation temperatures of 15 to 25 C (a range of 10 degrees) performed at test temperatures 10 to 30 C (Table 2). Sharp breaks in performance occurred at test temperatures near the upper and lower temperature extremes,

i.e., fish conditioned to 15, 20, and 25 C will swim at 10 C but not at 5 C; fish conditioned to 20, 25, and 30 C will swim at 30 C but not at 35 C.

The performance of individuals within each group (usually 10 fish) was least consistent at the upper and lower extremes of test temperatures (see Coefficient of Variation in Table 1). Performance was most consistent among fish at the next to the highest test temperature at which they swam and was not necessarily consistent, as might be expected, at their acclimation temperature.

DISCUSSION

The swimming speed at which fry were displaced from the test chamber was used, rather than the maximum speed maintained for the test period, because of the interest in applying the laboratory tests to the displacement of fry in streams. The speed that could have been maintained was between the displacement speed and the preceding (lower) test speed. Since the test speeds were increased at steps of approximately 22 mm/second, the speed that could have been maintained was approximately 11 mm/second less than the recorded displacement speed, assuming that it was roughly midway between the two. The difference may partly account for our measured speeds being higher than those recorded for other fishes by Bainbridge (1958) and others.

The testing procedure brought results that were reasonable and consistent except for one trial that appeared to be out of agreement. Smallmouth bass fry acclimated to 15 C and tested at 10 C were displaced at a speed lower than expected (Table 1, footnote) and inconsistent with other data. If the results for all tests at 10 C are plotted with speed against acclimation temperature, one sees that fry acclimated to 15 C did not perform as well as those acclimated to 10 or 20 C. The form of the curve, when compared with the curves for other test temperatures, shows that the swimming speed for fish acclimated to 15 C and tested at 10 C is inconsistent with the others. The extrapolated line in Figure 2 expresses a more reasonable relationship than is shown by the empirical data. This trial was one of the first to be conducted, so that the methods

may not have been mastered at that time. The discrepancy was discovered too late for us to repeat the test.

The displacement speeds recorded in these tests were similar to those recorded in a straight flume positioned in a small creek from which bass fry were taken and used for testing. These field measurements were influenced, of course, by uncontrollable natural fluctuations of stream temperatures. Water temperatures during the tests ranged from 20 to 25 C, while the water temperatures during the nights preceding the tests ranged about 5 C lower (15 to 20 C). Under these conditions, fry were not able to maintain a steady position for more than one minute at velocities above 240 mm/second. This speed falls between the maximum speeds recorded in the annular tank (Table 1) for temperatures of this range, that is, 190 mm/second for fish acclimated to 15 C and tested at 20 C, and 268 mm/second for fish acclimated to 20 C and tested at 25 C.

A comparison of speeds among fish of very different sizes can best be expressed in fish lengths traveled per unit of time. Gray (1957) estimated that a small freshwater fish could attain only briefly a maximum speed of above 10 times its length per second. Although Bainbridge (1958) concurred with this estimated maximum, he cited speeds of several species that had exceeded 10 lengths/second in bursts of a few seconds durations and reported his observations of 3.6-cm dace, *Leuciscus leuciscus*, attaining 20 lengths/second. He pointed out that the smaller specimens reached the highest relative speeds. Data on several marine fishes measured by Blaxter and Dickson (1959) also showed that the smaller individuals can swim relatively faster than larger ones. Two 15-cm trout, *Salmo trutta*, at 19 C attained speeds of 20 times their length/second. Dow (1962) timed river herring, *Alosa* (= *Pomolobus pseudoharengus* (Wilson)), moving through a sluice and found 28- to 31-cm individuals able to maintain speeds of 15-16 fish lengths/second for several seconds. He concluded that river herring may be able to swim better than laboratory studies suggest.

In another series of early tests in a labora-

tory flume, 14-mm bass fry acclimated to 23 C and tested at that temperature readily moved up a current of 182 mm/second over a smooth metal bottom. Such a speed constituted 13 lengths/second for these small fish. One fry moved a distance of 1 meter against a velocity of 264 mm/second, a speed equal to 19 lengths/second. Although the pygmy current meter used to measure these velocities could not measure flow within a few millimeters of the bottom where the fry were swimming, it seems that friction of the smooth metal could not have provided the small fry a significant reduction in current. Other tests in our laboratory suggest that 13 lengths/second can be maintained for several minutes at the higher (25 or 30 C) temperatures.

Published records we have cited and records of bass in our other experiments mentioned above indicated that the speeds given in Table 1 are not unreasonable. Although the speeds in excess of 10 lengths/second are certainly high to be maintained for nearly 3 minutes (the interval of velocity increases), one should accept the suggestion that small fish tend to attain higher relative speeds than larger ones and that these small fry were robust, well muscled, and of a vigorous-swimming species. They were similar in body form to the juvenile striped bass, *Roccus saxatilis* (Walbaum), tested by Kerr (1953). Eighty per cent of the striped bass, 1-inch average length, were still swimming at the end of 10 minutes at 1 foot/second (12 lengths/second), and 5% were still swimming at nearly 1.4 feet/second (18 lengths/second).

As might be expected and has been pointed out in most measurements of fish activity, the maximum speed that can be maintained is directly related to time. Endurance influences maximum swimming performance, at least beyond burst efforts of a few seconds. Endurance is, in turn, related to the size of the fish, its previous swimming experiences (to strengthen or to fatigue its body), acclimation, and the ambient water conditions. The metabolic limitations imposed on swimming have been extensively studied, mostly in Canadian laboratories. The work of Brett (1964, 1965, and in many other papers) on the Pacific salmon well illustrates the intensity of

experimentation and interpretation that has accompanied the Canadian work.

We have not measured the metabolism of our swimming bass fry, so we can only conjecture relationships to studies of other species. Working with sockeye salmon, *Oncorhynchus nerka*, Brett (1965, p. 1,500) found "rapid decay in the relative ability to maintain a sustained speed as size increases." He concluded: "The metabolic process is not a match for the great energy cost of sustained high speed for large fish." In principle, this is support for the assumption that the small-mouth bass were able to maintain relatively high speeds partly because they were small. One must keep in mind that we are referring to speed and endurance in units of fish length and are not implying that these small bass swim faster or longer than larger ones. Certainly the 22-mm bass would have more trouble in maintaining their positions in the high velocities of a flooded stream than would the larger members of the population. Absolute performance improves with size, as was illustrated by Boyar (1961) who figured that endurance in *Clupea harengus harengus* Linnaeus was a function of approximately the fourth power of length.

There was some evidence that the bass fry in our tests were not swimming to exhaustion except possibly at the very extremes of the temperature ranges. First, we found no difference in the displacement speed of fry that were carried through the testing sequence over somewhat shorter or longer periods of time. Second, at most temperatures, mortality rates of the fry following their tests were low. However, considerable mortality occurred following tests at extreme temperatures, suggesting that the fry had suffered exhaustion.

The curves plotted in Figure 2 are similar to those shown by Fry and Hart (1948) for the goldfish, *Carassius auratus* Linnaeus. One of the most interesting similarities is in the lines representing fish acclimated to the highest temperature, which in both studies was 35 C. The lines continued to rise with increased test temperatures. The goldfish were tested up to 38 C which was, according to Fry, Brett, and Clawson (1942), within 3 C of their upper incipient lethal temperature. The best

performance for both species acclimated to 35 C was considerably less than for fish acclimated to the next lower temperature. Fish acclimated to these extremely high temperatures might have been expected to perform better at somewhat lower, more moderate temperatures, away from the stress encountered near their lethal limits. This they did not do. They might have done so, however, in longer performance tests involving extreme levels of endurance and fatigue.

The performance curve for fry acclimated to 30 C was similar in one respect to the curve for fry acclimated to 35 C in that these groups showed the same abrupt decline in performance at lower test temperatures. They swam only at test temperatures of 5 and 10 degrees below their acclimation temperatures, whereas fish acclimated to 25 C swam at test temperatures 20 C below their acclimation temperature.

With a few exceptions, only fish acclimated to 35 C swam at 35 C. Fish acclimated to 30 and 25 C could not remain oriented at 35 C and those acclimated to 20 C would not swim. Exceptions did occur. One fry acclimated to 30 C swam very well at 35 C. A few fry acclimated to 25 C were induced to swim at 35 C but died soon afterwards.

Swimming performance of the smallmouth bass fry dropped off more rapidly at test temperatures above that of the peak swimming speed (Figure 2) than it did in the goldfish of Fry and Hart (1948) and was much like the abrupt decline in performance recorded by Roots and Prosser (1962) for the green sunfish, *Lepomis cyanellus* Rafinesque. Roots and Prosser (1962) found that the muscles and nerves of the green sunfish remained electrically excitable at the upper and lower limiting temperatures but coordinated reflexes, such as swimming, were blocked. Our fry could likewise swim erratically in short efforts beyond the temperatures at which they could maintain controlled swimming.

The range of acclimation and test temperatures used in these laboratory experiments more than covered the fluctuations of temperatures that occurred over several years during the bass spawning seasons in Stony and Jordan creeks, two east-central Illinois bass

streams. Assuming that mean daily water temperatures were associated with acclimation of the fry and the maximum or minimum daily temperatures represented test temperatures having the greatest influence on swimming, we then scanned the records for this period for mean temperatures and for low and high temperatures showing the greatest deviation from the means. During a three-year period we found no mean temperatures in Stony Creek, the larger of the two streams, as high as 30 C and very rarely 25 C. In the smaller Jordan Creek, during two years of recording immediately downstream from an exposed portion of the stream, a 30 C mean was recorded for only three exceptionally hot days in late July. Means of 24 C were not recorded in May but were found in the following number of days during June, July, and August, respectively, of 1951: 14, 14, and 8; and of 1952: 5, 20, and 12.

These records indicate that fry would not be acclimated to temperatures as high as 25 C until late in the bass nesting season. The minimum temperatures found during the bass nesting season, even among the extreme records at the Jordan Creek station, were slightly above 10 C in May and 15 C in June. Thus, the smallmouth bass fry in May might be acclimated to 20 C and exposed to temperatures as low as 10 C and in June acclimated to 25 C and exposed to 15 C. In either sequence of acclimation and exposure, the fry would be able to swim actively but their maximum speed would be reduced approximately one-half (Figure 2).

Since fish acclimate to high temperatures rather quickly, it is possible that an effective amount of acclimation took place during the 3- or 4-hour periods of 30 C water that occurred rather commonly in these streams during the summer months. If acclimated to 30 C, the bass fry would have swimming difficulties following a drop of any more than 10 C because of the rapid decline in performance at lower temperature of fry conditioned to 30 and 35 C (as discussed earlier and shown in Figure 2). On 22 July 1952, Jordan Creek temperatures reached 36.5 C and dropped that night to 23 C. The drop of more than 13 C from such a high temperature might have

blocked the swimming of bass fry but these temperatures and other such examples have been recorded only at times when the bass were too large to be vulnerable to such physical influences.

Acclimation to low temperatures and subsequent exposure to high temperatures would not be expected to reduce swimming abilities of bass fry in our test streams. The sequence of temperatures referred to above, if reversed, acclimated to 10 and exposed to 20 C, acclimated to 15 and exposed to 25 C, would actually improve the swimming performance (Figure 2).

Although the extremes of 5 and 35 C in our laboratory tests are near the lower and upper incipient lethal temperatures (roughly 4 and 38 C as found in unanalyzed data of Larimore and Childers), stream temperatures did not approach these levels during the season of bass reproduction, so direct mortality from high or low temperatures was not expected. Changes in the laboratory from 28 to 12 C, about the maximum that has been observed in these streams at this season, caused no fry mortality.

The rate of temperature change in natural waters would not noticeably alter swimming abilities nor cause mortality of fry. In the laboratory experiments, changes in water temperatures were more rapid than would be expected in our streams, and the fry showed no effects of the change.

We are ready to assume that there is no mortality nor inability to swim directly due to temperature changes that occur naturally in midwestern streams during the season of bass nesting and early growth. There is a significant reduction in swimming ability, however, with temperature drops of more than 10 C. The practical question then becomes how fast do the fry have to swim to maintain their position in the stream during periods of moderate flow or floods. Fry of this size (20–25 mm) from any acclimation temperature cannot swim much over 200 mm/second at 20 C. This velocity and much higher ones are common in areas of most bass streams. The small fry avoid these currents and venture into them only for brief bursts of swimming. When the stream is in flood stage, the entire

water mass of the main channel may be moving at this velocity. Smallmouth bass fry, under these conditions, would have to seek quieter waters at the side of the channel or behind protective objects in the stream. They do this but meet difficulties with the shifts in flow and the increase in turbidity associated with stream flooding, as will be discussed in other papers dealing with velocity, turbulence, and turbidity. Temperature changes may not directly cause the displacement of smallmouth bass fry, but the reduction in swimming ability associated with declining temperatures contributes to displacement of fry exposed to other physical changes accompanying flood waters.

ACKNOWLEDGMENTS

Support of this study was shared by the Illinois Department of Conservation, with funds from Federal Aid in Fish and Wildlife Restoration Project F-16-R, and the Illinois Natural History Survey. David McGinty and Rollin D. Andrews III, at that time employed by the Department of Conservation and the Survey, respectively, helped collect the bass fry used in experiments. Harold Humphreys, Illinois Water Survey, helped evaluate the flow characteristics in the experimental chamber.

Dr. George W. Bennett, Dr. William F. Childers, Dr. George Sprugel, Jr., and Mr. Owen F. Glissendorf, of the Survey, and Dr. C. Ladd Prosser and Dr. Arnold M. Sutterlin of the University of Illinois, read and criticized the manuscript.

LITERATURE CITED

- BAINBRIDGE, RICHARD. 1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tailbeat. *J. Exp. Biol.* 35: 109-133.
- BLAXTER, J. H. S., AND W. DICKSON. 1959. Observations on the swimming speeds of fish. *J. Cons. int. Explor. Mer.* 24: 472-479.
- BOYAR, H. C. 1961. Swimming speed of immature Atlantic herring with reference to the Passamaquoddy Tidal Project. *Trans. Amer. Fish. Soc.* 90: 21-26.
- BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Can.* 21: 1183-1226.
- . 1965. The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* 22: 1491-1501.
- , M. HOLLANDS, AND D. F. ALDERDICE. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Can.* 15: 587-605.
- CLEARY, ROBERT E. 1956. Observations on factors affecting smallmouth bass production in Iowa. *J. Wildl. Manag.* 20: 353-359.
- DOW, ROBERT L. 1962. Swimming speed of river herring *Pomolobus pseudoharengus* (Wilson). *J. Cons. int. Explor. Mer.* 27: 77-80.
- FRY, F. E. J., AND J. S. HART. 1948. Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Bd. Can.* 7: 169-175.
- , J. R. BRETT, AND G. H. CLAWSON. 1942. Lethal limits of temperature for young goldfish. *Rev. Can. Biol.* 1: 50-56.
- GRAY, J. 1957. How fishes swim. *Sci. Amer.* 197: 48-54.
- HAMMOND, B. R., AND C. P. HICKMAN, JR. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate, and glucose in rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Can.* 23: 65-83.
- KERR, JAMES E. 1953. Studies on fish preservation at the Contra Costa Steam Plant of the Pacific Gas and Electric Company. *Calif. Fish & Game Dept., Fish Bull.* 92, 66 p.
- MACLEOD, J. C. 1967. A new apparatus for measuring maximum swimming speeds of small fish. *J. Fish. Res. Bd. Can.* 24: 1241-1252.
- ROOTS, BETTY I., AND C. LADD PROSSER. 1962. Temperature acclimation and the nervous system in fish. *J. Exp. Biol.* 39: 617-629.
- ROUSE, HUNTER. 1946. *Elementary mechanics of fluids.* John Wiley & Sons, Inc., New York, N. Y.
- RYLAND, J. S. 1963. The swimming speeds of plaice larvae. *J. Exp. Biol.* 40: 285-299.