THERMOREGULATORY BEHAVIOR AND DIEL ACTIVITY PATTERNS OF BLUEGILL, LEPOMIS MACROCHIRUS, FOLLOWING THERMAL SHOCK

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ABSTRACT

Individual bluegill were allowed to thermoregulate for 3 days in a temperature-preference apparatus and then were exposed for 30 min to one of three temperature treatments: 21.0° , 31.0° , or 36.1° C. Fish exposed to 31° C served as controls for handling procedures. Thermoregulatory performance of surviving fish was monitored for an additional 3 days. Pretreatment results indicated mean lower and upper avoidance temperatures of 29.3° and 33.1° , and 31.2° C as the midpoint of the preferred range. All 20 fish exposed to 21° and 31° C survived treatment and demonstrated no significant differences between pretreatment and posttreatment thermoregulatory performance. Thirty-five percent of fish (7 of 20) exposed to 36.1° C died during treatment. Fish surviving the 36.1° C treatment retained the ability to thermoregulate; however, their mean lower and upper avoidance temperatures increased 0.6° and 0.7° C, respectively. Activity patterns were typically diurnal, but variable, in all three treatment groups. Immediately after treatment, the activity of fish exposed to 21° and 36.1° C was markedly decreased. Thereafter, activity tended to be higher in the 21° C group and lower in the 36.1° C group than during the pretreatment period.

Opportunities for temperature shock occur wherever sharp temperature gradients are present. Fish may be exposed to a sudden temperature change when penetrating the thermocline; in areas containing springs, upwellings or natural allochthonous inputs of water; in sharp horizontal temperature gradients characteristic of shallow waters; and during the passage of weatherfronts. Also, fish species migrating through or residing within waters under the influence of electric generating companies may be subjected to sudden temperature changes.

Investigations concerning thermal shock of fishes have mainly been limited to descriptions of morbidity stages and determinations of species' lethal temperatures. Noteworthy exceptions are studies by Sylvester (1972) and Coutant (1972a, b, 1973) that demonstrate enhanced vulnerability of thermally stressed fishes to predation. Fish mortalities owing to natural and artificially induced temperature shock have been reported in marine, estuarine, and freshwater environments (Gunther, 1936; Gunter, 1941; Huntsman, 1942; Gunter and Hildebrand, 1951; Bailey, 1955; Threinen, 1958; Colton, 1959; Alabaster, 1963; Clark, 1969), but the majority of work has involved laboratory determinations of thermal resistance.

An important question is: does a sublethal temperature shock disrupt subsequent thermoregulatory behavior of a fish? The objective of this study was to assess effects of temperature shock upon the thermoregulatory ability, selected temperatures, and locomotor activity patterns of individual bluegill, *Lepomis macrochirus*.

MATERIALS AND METHODS

Specimen

Juvenile bluegill (mean length 86.3 mm, range 72-105 mm) were captured during summer with electroshocking gear from Lake Wingra (Dane County, Wis.) and maintained in the laboratory at 25° C under constant photoperiod (LD 14:10 with 0.5 h dawn and dusk intervals) for at least 2 wk prior to experimentation. Throughout the preexperimental and experimental periods fish were fed pelleted food daily at 1630 h ± 15 min.

Apparatus

The thermoregulatory apparatus was derived from that of Neill and Magnuson (in press) with temperature control and rate-change modi-

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fications reported by Beitinger et al. (in press). The design (Neill, Magnuson, and Chipman, 1972) substitutes a temperature gradient over time for the spatial gradient typical of most temperature preference studies and allows an individual fish to serve as its own tank thermostat. Each 50-liter test tank was divided into halves with a molded fiber glass partition. A tunnel in the partition allowed the fish to choose between halves differing by a fixed 2°C temperature interval. When a fish selected the higher temperature, the temperature of the tank increased at a constant rate of 3°C/h while the 2°C differential between halves remained constant. When the fish moved to the cooler tank half, the temperature decreased at the same rate (3°C/h) until the fish again moved to the warmer tank half. By moving from one side to the other, a fish was able to control the temperature to which it was exposed. For this study, a potential temperature range of 4° to 55°C was available.

Temperatures of each tank half were monitored by a thermistor-wheatstone bridge circuit connected to a multichannel analog recorder. Avoidance temperatures (i.e., turnaround temperatures), preferred temperature range and midpoint of the preferred range (midpoint temperature) were the same as defined by Neill and Magnuson (in press). During the experiment, tunnel passes, recorded on an event recorder, were utilized as a measure of fish activity.

PROCEDURE

One fish was introduced per tank and allowed to experience the static system for 2.5 days with the tank halves set at 24° and 26°C. The test period

then began and tank temperature control was relinquished to each fish. Thermoregulatory performance during the second, third, and fourth days constituted the pretreatment data. Then fish were removed and individually subjected to a sudden temperature change in 3.5-liter cylindrical chambers. The water in each chamber was well aerated and "conditioned" with 150 ml of that fish's thermoregulatory tank water. High temperature treatment was 36.1 ± 0.1 °C and low temperature treatment was 21.0 ± 0.1 °C. For control purposes, a third group of fish was treated at 31.0± 0.1C, a temperature approximating the preferred range midpoint for bluegill. A series of cursory experiments indicated that fish body temperatures equilibrated to the treatment temperature during exposure. Fish were randomly allocated to the three treatment temperatures. Following a 30-min exposure, each surviving fish was returned to its respective thermoregulatory tank for an additional 3-day posttreatment period. Thermoregulatory tank temperatures at fish reentry were the same as those at fish removal. Finally, fish were isolated and observed for 1 wk for possible latent effects.

RESULTS

Prior to treatment, there were no statistically significant differences in thermoregulatory performance among the three groups (Kruskal-Wallis one way analysis of variance; Siegel, 1956; lower and upper avoidance temperatures, midpoint temperature, and width of preferred range, all P>0.20). Fish had mean lower and upper avoidance temperatures of 29.3° and 33.1°C and mean preferred range width of 3.8°C. The

TABLE 1.—Lower and upper avoidance temperatures, preferred range midpoint and width, pretreatment and posttreatment, for each of the three groups. Means ± standard deviations are given.

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Item	Controls 31.0°C	Cold shocked 21.0°C	Heat shocked 36.1°C	Grand mean
N	10	10	112	
Lower avoidance temperature, °C:				
Pretreatment	29.4 ± 0.7	29.2 ± 0.9	29.4 ± 0.9	29.3
Posttreatment	29.4 ± 0.8	29.1 ± 1.0	30.0 ± 0.8	
Upper avoidance temperature, °C:				
Pretreatment	33.1 ± 0.6	33.1 ± 0.5	33.1 ± 0.9	33.1
Posttreatment	33.1 ± 0.7	33.1 ± 0.5	33.8 ± 0.9	
Midpoint of preferred range, °C:				
Pretreatment	31.3 ± 0.6	31.2 ± 0.6	31.2 ± 0.8	31.2
Posttreatment	31.2 ± 0.7	31.1 ± 0.7	31.9 ± 0.8	
Width of preferred range, °C:				
Pretreatment	3.7 ± 0.6	3.8 ± 0.7	3.7 ± 0.7	3.7
Posttreatment	3.6 ± 0.5	4.0 ± 0.8	$3.8\pm\ 0.5$	3.8

¹One fish survived treatment but died during the first posttreatment night, owing to electronic failure.

BEITINGER: THERMOREGULATORY BEHAVIOR OF BLUEGILL

midpoint of the preferred range was 31.2°C (Table 1).

Pretreatment and posttreatment comparison of preferred range midpoints for individual fish are illustrated in Figure 1. Of the 20 control and coldtreated fish (1b, a), 18 had posttreatment midpoint



FIGURE 1.—Mean preshock and postshock midpoints of preferred range for individual bluegills in each of the treatment groups. Points falling on the 45° line indicate no change in midpoint temperatures.

temperatures within 0.3° C of their pretreatment values. None of the individual control fish had significant pretreatment and posttreatment changes in mean avoidance temperatures (*t*-test, P>0.05). Among the cold-treated fish, two had significant downward changes in lower avoidance temperatures and one had a significant downward change in its upper avoidance temperature. In the control and cold-treated groups, five fish each had lower posttreatment midpoint temperatures; however, there were no significant trends (Wilcoxon matched pairs, signed ranks; controls and cold-treated P>0.10).

Eleven of the twelve heat-treated fish had higher posttreatment midpoint temperatures (Figure 1c). This trend was highly significant (Wilcoxon matched pairs, signed ranks, P < 0.01). The mean posttreatment midpoint temperatures for heat-treated fish during each of the 3 days were 31.9° , 32.0° , and 31.9° C, indicating no return towards the pretreatment preference level.

Whereas all of the control and cold-treated fish survived the treatment process, 7 of the 20 fish (35%) exposed to 36.1°C died during treatment. All fish that died lost equilibrium early in the treatment and were dead within 5 min. The mean pretreatment midpoint temperature of those that died was significantly lower than that of the survivors (Mann-Whitney U test P < 0.05); however, temperatures experienced immediately prior to exposure were the same for both groups.

Although visual observations during the posttreatment period of this study were limited to avoid disturbing the fish, the typical immediate posttreatment behavior of both the heat- and cold-treated fish was submissive; often fish were hiding behind objects in their experimental tanks. However, at the feeding time, 4.5 h following exposure, nearly all fish actively fed.

A distinct diurnal pattern of activity was observed for each of the treatment groups throughout the 6-day experiment (Figure 2). Daytime hourly activities were typically two to three times higher than nighttime activities. The median activity (tunnel passes) of the cold- and, particularly, heat-treated fish dropped appreciably the hour following exposure (Figure 2). For general activity comparisons (Figure 3a, b) diurnal and nocturnal periods were separately analyzed (dawn and dusk excluded). With the pretreatment activity of each group serving as its own control, a series of Mann-Whitney U tests, with ties correction and z transformation were performed



FIGURE 2.—Median hourly tunnel passes by fish throughout the entire 6-day experiment for each treatment group. The arrow indicates time of treatment.

to compare the 3-day pretreatment and 3-day posttreatment median hourly activities. The pretreatment and posttreatment activity levels of the control group were not significantly different. The daytime posttreatment activity of coldtreated fish, although higher and more variable, was not significantly changed; however, night activity increased (P < 0.001). Heat-treated fish demonstrated the greatest change in activity. Both night and daytime activities decreased (P < 0.01, P < 0.001 respectively).

DISCUSSION

Combined pretreatment data demonstrate that the 32 test bluegills maintained their environmental temperatures within well-defined limits relative to the available temperature range. The



FIGURE 3.—Medians (circles) and 95% confidence limits for pretreatment and posttreatment bluegill hourly activities for the three treatment groups. Day and night activities are presented separately.

calculated midpoint of the preferred range, 31.2°C, is similar to that of Neill and Magnuson (in press), 30.4° and 0.8°C below the final temperature preferendum for bluegill reported by Fry and Pearson (1952).² The effect of sudden temperature stress on thermoregulatory behavior has not been previously examined. However, several other external factors have been reported to influence temperature preferenda, including season (Sullivan and Fisher, 1953; Zahn, 1963; Barans and Tubb, 1973), light intensity (Sullivan and Fisher, 1954), starvation (Javaid and Anderson, 1967) and exposure to chlorinated hydrocarbons (Ogilvie and Anderson, 1965; Peterson, 1973).

Pretreatment and posttreatment comparisons in the grouped control data clearly indicate no change in thermoregulatory performance. The Δt experienced by control fish was minimal and changes, if any, could be ascribed to handling or time-dependent variations in temperature preference.

Cold- and heat-treated fish actually experienced two temperature shocks. One occurred when the fish were introduced into the treatment chambers and the second when they were returned to their experimental tanks. Both cold and heat treatments were conducted at temperatures actively avoided by fish while in their thermoregulatory tanks.

Cold exposure did not significantly change any of the four measured parameters of thermoregulatory behavior. These fish experienced a Δt of approximately 10°C, but the exposure temperature, 21°C, is near the middle of the tolerance zone for bluegill. That these fish did not select lower temperatures was expected, owing to the slow rate of downward temperature acclimation characteristic of fishes (Brett, 1944, 1946). The lethal rates of temperature increase are at least 20 times the corresponding lethal rates of temperature decrease for bluegill (Speakman and Krenkel, 1971). Apparently, the 30-min exposure was not sufficient to change the acclimation state and, hence, the preferred temperature range of these fish.

Fish exposed to 36.1°C experienced a smaller Δt (about 5°C) during treatment, but this exposure was to within approximately 0.5°C of the bluegill's incipient upper lethal temperature (Hart, 1952; Cairns, 1956). The ability of surviving bluegills to thermoregulate was not deleteriously affected by the 30-min exposure to 36.1°C, however, statistically significant changes in avoidance and midpoint temperatures did occur. Thus, the thermoregulatory performance of bluegill was influenced more by exposure either to 1) temperatures closer to lethal limits than exposure to large Δt 's per se or to 2) temperatures above rather than those below, the acclimation state of the fish.

Of the three exposure temperatures, only 36.1° C resulted in fish mortality. The pretreatment midpoint temperatures of these fish were significantly lower than those of fish surviving heat treatment, indicating a relationship between preferred and upper lethal temperatures. That a considerable proportion, 35%, of fishes exposed to 36.1° C died, is more important to the population than the observation that surviving

²Fry, F. E. J., and B. Pearson. 1952. Some temperature relations of the pumpkinseed and bluegill sunfish. Unpubl. manuscr., 10 p. Ont. Fish. Res. Lab. R.R. 2, Maple, Ont., Can.

fish had a 0.7°C increase in preferred range following exposure.

Use of tunnel passes as an index of locomotor activity is discussed by Beitinger et al. (in press). The diurnal activity pattern continued after treatment in all three groups (Figure 2). Immediately subsequent to treatment, a marked decrease in activity occurred in cold- and heat-treated fish but not in the control group (Figure 2). This decrease might help explain the increased susceptibility of thermally shocked fish to predation reported by Coutant (1972a, b, 1973) and Sylvester (1973). Hocutt (1973) found that exposure to rapid temperature changes, as large as 12°C below and 8°C above ambient temperatures, resulted in decreased swimming performance in juvenile largemouth bass. Micropterus salmoides; spotfin shiner, Notropis spilopterus; and channel catfish, Ictalurus punctatus.

Due to their mobility and acute temperature sensitivity, fishes are able to avoid environments of unfavorable temperatures. If trapped at these temperatures, fish possess the ability to resist thermal death. Ecologically, resistance ability affords a fish the opportunity to escape potentially lethal conditions at least until they lose equilibrium. Fish are exposed to stressful conditions when existing within their thermal resistance zone or when experiencing large temperature changes. The major objective of this research was to examine the thermoregulatory performance of bluegill following "high" and "low" thermal exposure. Nevertheless, the 35% mortality among 36.1°C treated fish and the severe depression in immediate posttreatment activity of both the 21.0° and 36.1°C treated fish were the two most ecologically important findings. All fish surviving treatment retained the ability to behaviorally thermoregulate, hence, disruption of thermoregulatory behavior is not a likely outcome of thermal shock in fishes.

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LITERATURE CITED

- Alabaster, J. S.
 - 1963. The effect of heated effluents on fish. Int. J. Air Water Pollut. 7:541-563.
- BAILEY, R. M.
 - 1955. Differential mortality from high temperature in a mixed population of fishes in southern Michigan. Ecology 36:526-528.

BARANS, C. A., AND R. A. TUBB.

- 1973. Temperatures selected seasonally by four fishes from Western Lake Erie. J. Fish. Res. Board Can. 30:1697-1703.
- BEITINGER, T. L., J. J. MAGNUSON, W. H. NEILL, AND W. R. SHAFFER.
 - In press. Behavioural thermoregulation and activity patterns in the green sunfish, *Lepomis cyanellus*. Anim. Behav.

BRETT, J. R.

- 1944. Some lethal temperature relations of Algonquin Park fishes. Univ. Toronto Stud. Biol. 52., Publ. Ont. Fish. Res. Lab. 63:5-49.
- 1946. Rate of gain of heat-tolerance in goldfish (*Carassius auratus*). Univ. Toronto Stud. Biol. 53, Publ. Ont. Fish. Res. Lab. 64:9-28.
- CAIRNS, J., JR.
 - 1956. Effects of heat on fish. Ind. Wastes 1:180-183.

- 1969. Thermal pollution and aquatic life. Sci. Am. 220(3):19-27.
- COLTON, J. B., JR.
 - 1959. A field observation of mortality of marine fish larvae due to warming. Limnol. Oceanogr. 4:219-222.

COUTANT, C. C.

- 1972a. Effect of thermal shock on vulnerability to predation in juvenile salmonids. I. Single shock temperatures. U.S. AEC Res. Dev. Rep. BNWL-1521, 17 p.
- 1972b. Effect of thermal shock on vulnerability to predation in juvenile salmonids. II. A dose response by rainbow trout to three shock temperatures. U.S. AEC Res. Dev. Rep. BNWL-1519, 12 p.
- 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Board Can. 30:965-973.
- GUNTER, G.

1941. Death of fishes due to cold on the Texas coast, January, 1940. Ecology 22:203-208.

GUNTER, G., AND H. H. HILDEBRAND.

- 1951. Destruction of fishes and other organisms on the South Texas Coast by the cold wave of January 28-February 3, 1951. Ecology 32:731-736.
- GUNTHER, E. R.

1936. A report on oceanographical investigations in the Peru Coastal Current. Discovery Rep. 13:107-276.

HART, J. S.

1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. Univ. Toronto Biol. 60, Publ. Ont. Fish. Res. Lab. 72, 79 p.

Clark, J. R.

BEITINGER: THERMOREGULATORY BEHAVIOR OF BLUEGILL

HOCUTT, C. H.

1973. Swimming performance of three warmwater fishes exposed to a rapid temperature change. Chesapeake Sci. 14:11-16.

HUTSMAN, A. G.

- JAVAID, M. Y., AND J. M. ANDERSON. 1967. Influence of starvation on selected temperatures of some salmonids. J. Fish. Res. Board Can. 24:1515-1519.
- NEILL, W. H., J. J. MAGNUSON, AND G. G. CHIPMAN.
- 1972. Behavioral thermoregulation by fishes: A new experimental approach. Science (Wash., D.C.) 176:1443-1445.

- In press. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a power plant at Lake Monona, Wisconsin. Trans. Am. Fish. Soc.
- OGILVIE, D. M., AND J. M. ANDERSON.
 - 1965. Effect of DDT on temperature selection by young Atlantic salmon, *Salmo salar*. J. Fish. Res. Board Can. 22:503-512.

PETERSON, R. H.

1973. Temperature selection of Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) as influenced by various chlorinated hydrocarbons. J. Fish. Res. Board Can. 30:1091-1097.

SIEGEL, S.

1956. Nonparametric statistics for the behavorial sciences. McGraw-Hill, N.Y., 312 p.

SPEAKMAN, J. N., AND P. A. KRENKEL.

1971. Quantification of the effects of rate of temperature change on aquatic biota. Vanderbilt Univ., Dep. Environ. Water Resour. Eng., Rep. 6.

SULLIVAN, C. M., AND K. C. FISHER.

- 1953. Seasonal fluctuations in the selected temperature of speckled trout, *Salvelinus fontinalis* (Mitchill). J. Fish. Res. Board Can. 10:187-195.
- 1954. The effects of light on temperature selection in speckled trout Salvelinus fontinalis (Mitchill). Biol. Bull. (Woods Hole) 107:278-288.

Sylvester, J. R.

1972. Effect of thermal stress on predator avoidance in sockeye salmon. J. Fish. Res. Board Can. 29:601-603.

Threinen, C. W.

1958. Cause of mortality of a midsummer plant of rainbow trout in a southern Wisconsin lake, with notes on acclimation and lethal temperatures. Prog. Fish-Cult. 20:27-32.

Zahn, M.

1963. Jahreszeitliche Veränderungun der Vorzugstemperaturen von Scholle (*Pleuronectes platessa* Linne) und Bitterling (*Rhodeus sericeus* Pallas). Verh. Dtsch. Zool. Ges. p. 562-580. [Not seen, from Fry, F. E. J. 1969. *In* W. S. Hoar and D. J. Randall (editors) Fish physiology, Vol. VI. Academic Press, N.Y.]

^{1942.} Death of salmon and trout with high temperature. J. Fish. Res. Board Can. 5:485-501.

NEILL, W. H., AND J. J. MAGNUSON.