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SOME LETHAL TEMPERATURE RELATIONS OF ALGONQUIN PARK FISHES

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ABSTRACT

The upper lethal temperatures of six species of fish, including five Cyprinidæ and one Ameiuridæ, from Algonquin Park, Ontario, were determined at intervals of approximately two weeks, from the middle of May to the middle of September, 1941. The lethal temperature, defined as that temperature at which fifty per cent of the fish die if exposed for a period of twelve hours, rose with ascending lake temperature, reflecting the major changes in lake temperature by parallel changes in the lethal temperature.

The relation of both the upper and lower lethal temperatures of *Ameiurus nebulosus* for different temperatures of acclimation was established. From these results and experiments on the rate of adaptation to relatively high and low temperatures some indication of the relation of the lethal temperature to the natural environmental temperatures was obtained.

The upper lethal temperatures for thirteen species of fish and the lower lethal temperatures for eight of these were determined in the middle of the summer when the lake temperatures were approaching a maximum for the year.

INTRODUCTION

The existence of thermal adaptation and of changes in metabolism as a result of a change in thermal environment is a well-established phenomenon in nature. Belehradek (1935) has reviewed the subject very extensively. Thermal adaptation in fishes was demonstrated clearly by Loeb and Wasteneys (1912) when they showed that the duration of life of the common mummichog, *Fundulus heteroclitus*, at 31° C. could be extended from a fraction of an hour to an indefinite period of time by previously exposing the fish to a temperature of 27° C. for seventy-two hours. Hathaway (1927) obtained a difference of 5.2 centigrade degrees in the lethal temperature of the largemouth black bass, *Huro salmoides*, by acclimating this species to 10° C. and to 30° C. for four days. He showed that continued exposure to high or to low temperatures progressively raised or lowered the lethal temperature of each of four freshwater species studied. The course of temperature acclimation and changes in respiratory metabolism of the long-jawed goby, *Gillichthys mirabilis*, was followed by Sumner and Doudoroff (1938) over a total range of

20 centigrade degrees. A study of the relation between the lethal temperature and acclimation temperature in young goldfish, *Carassius auratus*, was carried out by Fry, Brett and Clawson (1942) and the complete field of thermal adaptation for this species explored.

Under normal conditions in north-temperate climates freshwater fish are exposed to wide variations of temperature throughout the course of a year, the major fluctuations taking place during the spring and summer months. In the lakes of Algonquin Park, Ontario, Lat. 46° N., Long. 78° W., the surface temperature of the water may rise from the freezing point in early May to well above 25° C. by late July. Since the lethal temperature of a fish may be changed by altering the acclimation temperature, it might be expected that the lethal temperatures of fish in Algonquin Park would show considerable change during the course of the year.

In order to ascertain the extent of the variation in the upper temperature tolerance among different species of fish in Algonquin Park lakes, lethal temperature experiments were performed regularly from May until late September, 1941, on some of the more common species available. While this investigation was concerned mainly with experiments to determine the changes in upper lethal temperature, it also dealt with some aspects of resistance to low temperatures and the problem of temperature acclimation.

The term "acclimation" has been used here in preference to "acclimatization" although there seems to be no clearly defined distinction between the two words, nor for that matter an adequate and clearly defined use of either term. Heilbrunn (1937) does not distinguish between the two, stating "acclimatization or acclimation has to do with the capacity of a living organism to become tolerant toward conditions of the external environment which are naturally injurious or fatal to it." In most organisms, however, adaptation takes place to meet all conditions of the external environment, whether naturally injurious or not. To obviate difficulties in the use of these words, only the term "acclimation" has been used and comprises the adaptation of an organism to any condition of its natural external environment

which may or may not be fatal and is used also to embrace conditions which were imposed experimentally and exceeded the limits in nature.

The stimulus for this work and the suggestion of the problem came from Dr. F. E. J. Fry. His opinions have been constantly sought and his criticisms were invaluable in writing the manuscript.

I am sincerely grateful to Professor W. J. K. Harkness, director of the Ontario Fisheries Research Laboratory, who has provided the means whereby this study was made possible and who has added his thoughtful advice.

To those members of the Laboratory who assisted in collecting the fish and aided in some of the routine experimental work, I extend my appreciation.

EXPERIMENTAL PROCEDURE

The method of lethal temperature determination used previously (Brett, 1941) was employed in this study. It is an adaptation of that introduced by Hathaway (1927) who expressed his results on the effects of high temperature as the maximum tolerance of an average of normal fish for different periods of time up to twenty-four hours. For comparative reasons and to establish a clearly defined and easily determined index, the lethal temperature was defined by the author in an earlier paper (1941) as that temperature at which fifty per cent of the fish die if exposed for a period of fourteen hours (reduced to twelve hours in this investigation).

In determining this index, aerated tanks two feet square and seven inches deep, coated inside with aluminum paint, were heated by means of Bunsen burners and the temperature maintained within ± 0.2° C. by adjusting the flame of the burner and checking the temperatures every ten to fifteen minutes. A sheet of galvanized iron, two inches below the tank, shielded the bottom from direct contact with the flame and distributed the heat evenly. As a routine, four tanks differing in temperature by 1° C. were used and the experiment continued for a period of twelve hours. In general ten specimens were placed in each tank;

however, if the fish were small, the number was sometimes increased to fifteen per tank. As the fish died they were removed from their respective tanks and kept for reference. To obtain the fifty per cent lethal point a survival curve was plotted, as in figure 1, from the results of a given experiment and the lethal temperature obtained by interpolation.

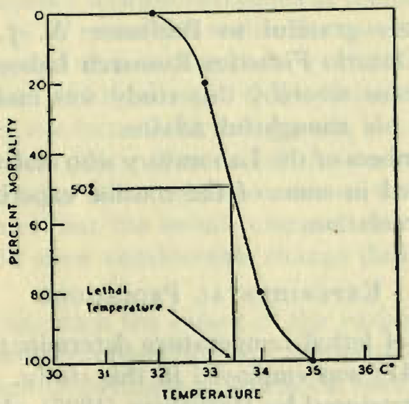

FIGURE 1.—Graphical method of determining the lethal temperature as adapted from Hathaway (1927). The points plotted were obtained from an experiment using forty bullheads caught on August 26, 1941. Each point represents the extent of mortality for ten bullheads at each of the temperatures indicated.

The species of fish used in the study of seasonal variation in the lethal temperature were obtained in abundance from two lakes, lake Opeongo and lake Amikeus. In each of these lakes was placed a recording thermometer with the bulb located in the region constantly used for trapping purposes. This situation for lake Opeongo was at the relatively shallow, marshy mouth of Costello creek which empties into the southern end, the maximum depth being approximately twelve feet: that for lake Amikeus was at the western end where the water was not more than four feet in depth. The means of the daily maximum and minimum temperatures from lake Opeongo were averaged in running groups of seven (figure 4). This smoothed average, which is referred to as "average temperature," has been used to

relate directly the changes in lethal temperature with the trends of change in lake temperature and to determine the degree of correlation of these two.

All the fish were caught by means of numerous cylindrical minnow traps placed at various depths and not more than fifteen feet from shore. These were set in the evening, using stale bread for bait, and lifted early the following morning, the catch being then transported in fish tanks by truck to the laboratory and experiments carried out immediately. Only in the case of rarer species, when insufficient numbers were obtained on the first attempts of collection, did any appreciable length of time (more than one hour) elapse from the lifting of the traps to the start of an experiment. Every effort was made to reduce this time to a minimum when determining the variation in seasonal lethal temperatures so that no effects of temperatures imposed in captivity were present. Experiments on the lethal temperature of a given species of fish were performed approximately every two weeks.

In these experiments attention was focused mainly on the direct effect of high temperatures which were not complicated by the possible secondary effects of disease arising from prolonged exposure to high, but sub-lethal temperatures. Since the results obtained for experiments of twelve hours' duration differed so slightly from those of fourteen hours, it was decided to reduce the time for the lethal temperature experiments to twelve hours, this length of time being better suited to the organization of the investigation.

Evidence that twelve hours is of sufficient length for determinations of this nature was obtained experimentally. In the case of yearling speckled trout, *Salvelinus fontinalis*, an experiment at the calculated lethal temperature of this species was carried out over a period of twenty-four hours on thirty-two fish. By the twelfth hour fourteen fish had died (44 per cent mortality). During the following twelve hours, only three more fish succumbed, raising the total mortality for the twenty-four hour period up to seventeen fish (53 per cent mortality). Twelve hours, therefore, gave a result which differed from that for twenty-four hours by only nine per cent. The lethal temperature, however, is determined graphically from a series of points which spread out over about 3° C., each representing the percentage of mortality at a given temperature. They include a variation from zero to one hundred per cent mortality. Where the mortality is one hundred per cent the question of the duration of the experiment does not arise. It only becomes a question for the intermediate points. Thus, on consideration of the fact that in an experiment at the lethal temperature of a species, if the temperature were raised by 1° C. the percentage of mortality would change from fifty to nearly one hundred, whereas for a drop of 1° C., it would approach zero, it may be concluded that the accuracy of this method must be within a small fraction of 1° C.

In such a system as that used for determining lethal temperatures the oxygen is continually being depleted by the respiration of the fish. This is partially replaced by the passage of oxygen from the air into the water. Since this is not sufficient to maintain the oxygen at an adequate level, it would become a limiting factor if no precautions were taken to keep up the oxygen saturation. To guard against oxygen deficiency compressed air was bubbled by two jets into each tank, and the percentage of oxygen present recorded at different times for each tank throughout an experiment. This percentage of saturation averaged in the region of seventy-five, but dropped down close to sixty in certain cases.

The problem of oxygen as a limiting factor was dealt with in two ways. Given that the system of circulation and aeration was not supplying enough oxygen and therefore affecting the lethal temperature, then by reducing the number of fish to one-half in each tank, thus increasing the amount of available oxygen, the lethal temperature should show a significant change. The same result could be obtained by bubbling oxygen instead of air into the water. Experimentally no change in the lethal temperature was obtained by using four yearling speckled trout per tank instead of eight, the usual number for that species (Brett, 1941). In regard to the second approach it was found that raising the oxygen saturation to three times that of air-saturated water by the use of compressed oxygen did not affect the lethal temperature of the bullhead. Increased oxygen saturation was also used in an attempt to raise the upper acclimation limit in young goldfish without success. Thus, at no time did oxygen become a limiting factor under the conditions of the experiment.

The bullheads, *Ameiurus nebulosus*, used in determining the relation of the upper lethal temperature to the acclimation temperature (p. 26) were transported in tanks from lake Opeongo, Algonquin Park, to Toronto late in September, 1940. By the middle of December the experiments on this group of fish were completed. Many attempts to feed the fish were made but with little or no success. In the rather confined space of the troughs no inclination was shown to feed on the fish food, liver, beef heart, or dead fish supplied. That this might have been a factor affecting the lethal temperature was considered, but no controls were available at that time. Since the results obtained were quite orderly and showed no unusual variations, it was assumed that starvation had no effect.

In order to provide evidence for this belief, on June 16, 1941, eighty bullheads were put in a large tank at the mouth of Costello creek, lake Opeongo, to undergo an extended period of starvation. This tank was open at the top and placed in such a position that the surface water could just wash over the edge, yet prevent the escape of any bullheads.

Of the eighty fish used, four died and five were removed before the end of the experiment because of signs of disease and *Saprolegnia* infection centred around a number of sores, probably caused by contact with the spines of other fish. The seventy-one remaining fish were used in two sets of lethal temperature experiments, the first after twenty-five days of starvation, the second after forty days of starvation.

In determining the effect of starvation on the lethal temperature it was imperative that the non-starved fish were of exactly the same acclimation as the starved fish. Three days before an experiment, bullheads were caught from Costello creek in the proximity of the starvation tank and these fish, along with thirty-five of the starved fish, were then transported to troughs supplied with a flow of lake water, tapped from a common source, and left there for the three-day period. These precautions were taken to eliminate any minor difference in acclimation of the two groups.

Experiments were carried out simultaneously with starved and non-starved fish, at equal temperatures. After an experi-

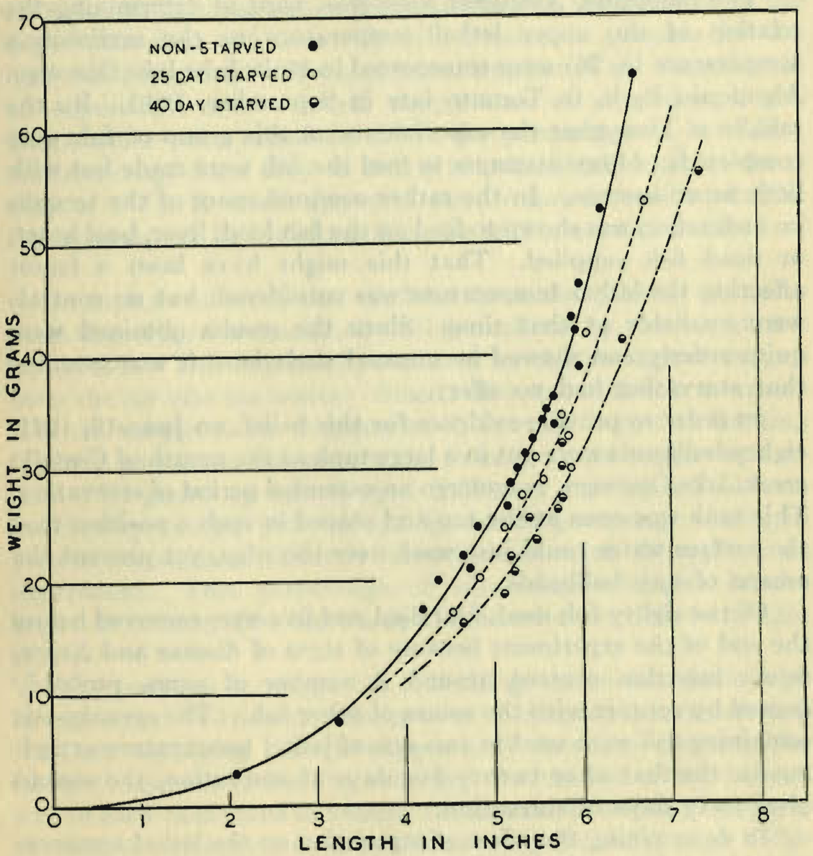

FIGURE 2.—Weight-length relation of starved and non-starved bullheads. Each point represents the average measurements of three fish.

ment all fish were weighed and measured. The weight-length relations of the three sets of fish (non-starved, twenty-five-day starved, forty-day starved) are plotted in figure 2. The effect of starvation is clearly indicated by the three distinct curves.

No appreciable difference in the lethal temperatures, even after forty days was obtained (table 1).

TABLE 1.—Results of lethal temperature experiments on starved and non-starved bullheads.

	Non-starved			25-day starved				Non-starved			40-day starved		
T° C.	No.	%	Hrs.	No.	%	Hrs.	T° C.	No.	%	Hrs.	No.	%	Hrs.
34.5	10	0	12.0	0	..	..	35.0	10	0	12.0	10	0	12.0
35.0	10	40	9.1	10	50	8.3	35.5	10	80	5.8	10	90	5.2
35.5	10	90	3.1	10	90	3.7	36.0	10	100	2.2	10	100	1.6
36.0	10	100	1.4	10	100	1.5	36.5	10	100	1.2	10	100	0.6

T° C.—Temperature of experimental tank.
No.—Number of fish per tank.
%—Per cent mortality.
Hrs.—Average survival time in hours.

On examining the starved fish after an experiment, no trace of food was found in any of the stomachs. In a few, slight traces of refuse were present in the lower portion of the intestine. Although no analysis was made, this refuse was probably composed of discharged gastric and intestinal epithelial cells. The fat bodies of the intestinal mesentery, usually very abundant, were completely absorbed, those of the gonad mesentery being lacking in all but one or two cases. The ovaries were apparently quite healthy, the majority of these fish having spawned earlier in the season. Although noticeably thin the general appearance of the starved fish was one of healthy activity.

This period of starvation did not visibly impair the health or activity of the fish and it may be concluded that for bullheads starvation for forty days at summer temperatures has no significant effect on their ability to resist high temperatures in experiments of twelve hours' duration.

In this study of lethal temperature relations of some Algonquin

Park fishes, thirteen species of fish were investigated. Close to 4,500 fish were used, involving ninety-one upper lethal determinations, fifteen lower lethal determinations, and two experiments on the rate of temperature acclimation. The following is a list of the thirteen species studied with the mean total length in inches of the specimens obtained.

Species	Mean length	Standard deviation
Salvelinus fontinalis (Mitchill), Common brook trout	5.69	± 1.28
Catostomus commersonnii (Lacépède), Common white sucker	5.39	± 0.54
Semotilus atromaculatus (Mitchill), Creek chub	4.74	± 0.89
Margariscus margarita (Cox), Pearl dace	3.10	± 0.46
Pfrille neogaea (Cope), Finescale dace	2.65	± 0.32
Chrosomus eos Cope, Northern redbelly dace	2.32	± 0.31
Notemigonus crysoleucas (Mitchill), Golden shiner	3.49	± 0.45
Pimephales promelas Rafinesque, Fathead minnow	2.38	± 0.41
Notropis cornutus (Agassiz), Common shiner	4.46	± 0.51
Ameiurus nebulosus (Le Sueur), Brown bullhead	5.38	± 0.66
Perca flavescens (Mitchill), Yellow perch	4.93	± 0.80
Lepomis gibbosus (Linnaeus), Pumpkinseed	4.00	± 0.42
Eucalia inconstans (Kirtland), Brook stickleback	2.20	± 0.28

SEASONAL VARIATION IN THE UPPER LETHAL TEMPERATURE

As previously stated, one of the main objectives was that of determining the lethal temperatures of fish taken directly from a lake at different times of the year and to discover what variations there might be in their temperature tolerance.

Experiments were begun on the bullhead in the middle of July, 1940, and continued until early in October of the same year. The study of this species was again commenced on May 15, 1941, and carried through the summer until September 12. The results showed definitely the existence of marked variations in the lethal temperature for fish from normal lake water (figure 3). The upper lethal temperature, starting from a high level in August, 1940, gradually fell off with the onset of the autumn season. When it was again picked up in the spring of 1941, the lethal temperature was on the rise and reached a peak near the end of July and then repeated the decline of the previous year (tables 2, 3). In all, the variation found in the upper lethal temperature was about 6.4 centigrade degrees.

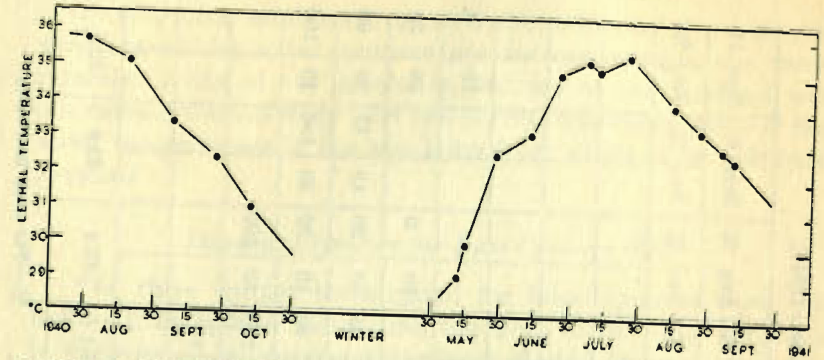

FIGURE 3.—Variation in the upper lethal temperature of *Ameiurus nebulosus*, from lake Opeongo, 1940 and 1941.

TABLE 2.—Seasonal variation in the lethal temperature of *Ameiurus nebulosus* (1940).

Date	July 29		Aug. 18		Sept. 8		Sept. 28		Oct. 12	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%
30									10	0
31									10	50
32					10	0	10	20	10	90
33					10	10	9	100	10	100
34	10	0	10	0	20	90	10	100		
35	10	10	10	40	10	100				
36	10	70	10	100						
37			10	100						
Lethal Temperature	35.7		35.1		33.4		32.4		31.0	

T° C.—Temperature of experimental tank.
No.—Number of fish used in each tank.
%—Per cent mortality.

TABLE 3.—Seasonal variation in the lethal temperature of *Ameiurus nebulosus* (1941).

Date	May 12		May 15		May 28		June 14		June 25		July 8		July 11		July 25		Aug. 15		Aug. 26		Sept. 6		Sept. 11	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
28	10	0																						
29	10	40	7	0																				
30	10	100	6	50																				
31	10	100	7	100	10	0	9	0															10	0
32			7	100	10	20	9	0											10	0			10	20
33					10	70	10	50	10	0							10	0	10	20	19	47	10	60
34					10	100	9	89	10	0	10	0	10	0	10	0	10	40	10	80	20	100	10	100
35							8	100	10	60	20	30	10	40	10	10	10	100	10	100				
36									10	100	10	100	10	100	20	75	10	100						
37									10	100	8	100			10	100								
Lethal Temperature	29.1		30.0		32.6		33.2		34.9		35.3		35.1		35.5		34.1		33.4		32.9		32.6	

T° C.—Temperature of experimental tank. No.—Number of fish used in each tank. %—Per cent mortality.

Having once established in 1940 the existence of a seasonal variation in the lethal temperature for one species, the more extensive study of five species in addition to the bullhead was commenced the following year and careful recordings made of the water temperatures in the two lakes from which these fish were obtained.

Seasonal Variation for Lake Opeongo Fish

The three species investigated for lake Opeongo were the bullhead, the golden shiner, and the creek chub. The variation in their lethal temperatures has been plotted in figure 4 and is represented by the three upper curves. In the same figure and for the same axes of temperature and time the averaged variation in lake temperature has also been included and appears as the lowest curve on the page.

By the last week in April of 1941 the ice had broken up in all the lakes of Algonquin Park and a rapid rise in temperature of the surface waters had begun. It was not until late in November of the same year that these lakes were once again completely frozen over. Since the maximum density of water occurs at 4° C. and it is not until the whole volume of water in a lake has reached this temperature that the surface water can continue its temperature fall to 0° C. and freezing, it may be concluded that, with the possible exception of spring-fed areas, no temperatures above 4° C. are experienced by the fish in these lakes as long as the surface is covered by a layer of ice. Thus, in figure 4, a dotted line has been used to indicate this 4° C. level for the winter months and also to indicate the rise and fall of temperature to and from the times when actual temperature recordings were made. In a later section it will be seen that the lethal temperature of the bullhead for an acclimation temperature of 4° C. is 28° C. Dotted lines have therefore been used to represent the lethal temperature of this species at 28° C. for the corresponding time of 4° C. in the lake water.

The changes in lethal temperature are relatively smooth by reason of the natural averaging factors of the rate of adaptation to low and to high temperatures and the extent of response to

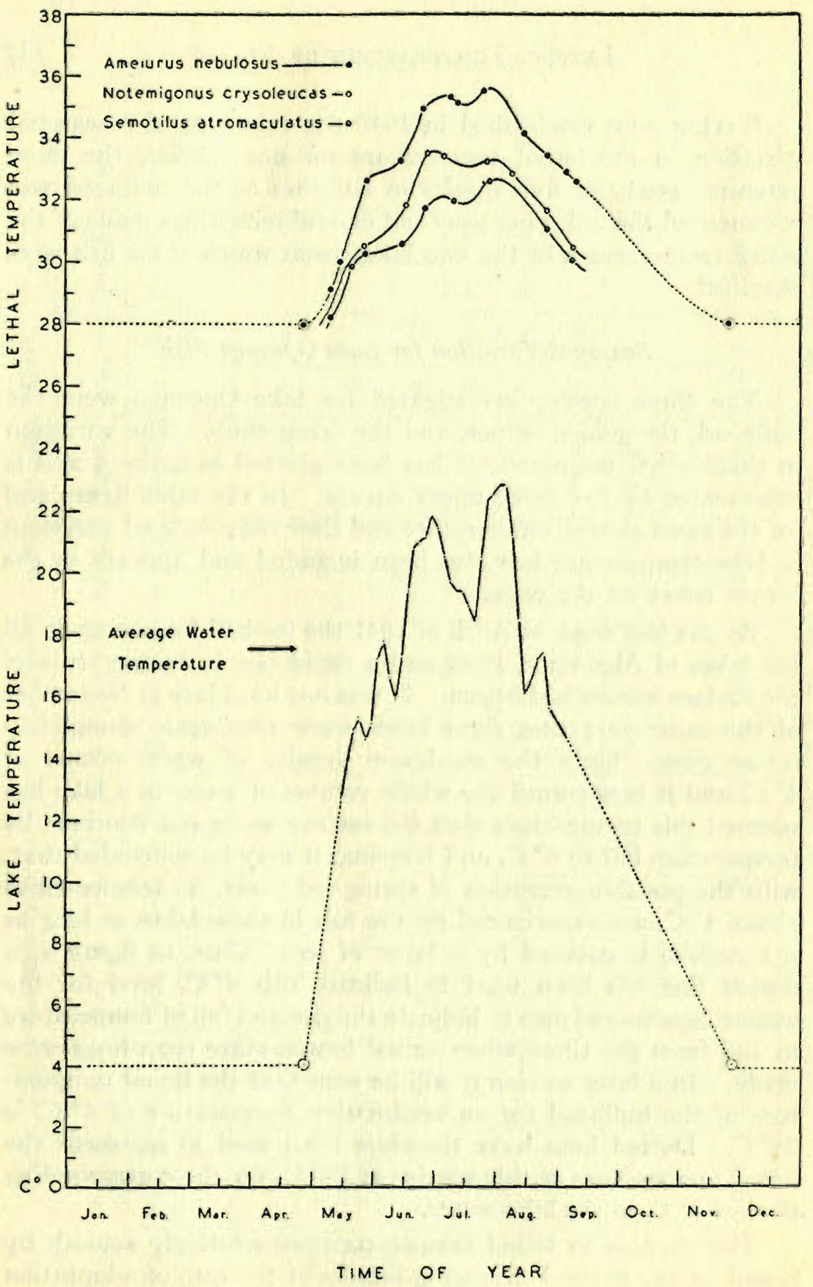

FIGURE 4.—Seasonal variation in the lethal temperature of three species from lake Opeongo, 1941, and the variation in the average temperature of the lake water.

TABLE 4.—Seasonal variation in the lethal temperature of *Semotilus atromaculatus* (1941).

Date	May 12		May 20		May 28		June 16		June 27		July 9		July 28		Aug. 25		Sept. 7	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
27	10	0																
28	10	10	4	0														
29	10	90	10	10													10	30
30			10	20	7	14	15	20							5	0	10	60
31			10	100	8	100	10	60	10	10	10	0			6	50	10	100
32					7	100	10	90	10	60	10	60	10	0	7	100	10	100
33					6	100	10	100	10	100	10	90	9	78	7	100		
34									10	100	10	100	10	100				
Lethal Temperature	28.2		29.9		30.3		30.6		31.8		32.0		32.6		31.0		30.0	

T° C.—Temperature of experimental tank.
No.—Number of fish used in each tank.
%—Per cent mortality.

TABLE 5.—Seasonal variation in the lethal temperature of *Notemigonus crysoleucas* (1941).

Date	May 28		June 17		June 28		July 8		July 28		Aug. 9		Aug. 26		Sept. 8	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
29	5	0													12	0
30	10	40	7	0											8	25
31	10	90	7	0									5	20	7	100
32	13	100	7	57	8	0	9	0	10	10			7	71		
33			10	100	9	11	9	33	9	44	7	57				
34					9	55	9	78	5	80	7	100				
35					8	100	9	100								
36							10	100								
Lethal Temperature	30.3		31.8		33.5		33.4		33.2		32.8		31.6		30.4	

T° C.—Temperature of experimental tank.
No.—number of fish used in each tank.
%—Per cent mortality.

thermal changes in the lake water. If the mechanical method of averaging the lake temperatures in running groups of seven was extended further, then the lake-temperature curve would take on the more smoothed appearance of that for the lethal temperature curve. The presence of dips and peaks in the lethal temperature curves is indicative of the sensitivity and high degree of flexibility of the lethal temperature. The three upper curves nearly parallel each other since the response of the lethal temperature for each of these species is practically identical for the same change in lake temperature. These fish possess what might be termed an "average type" of response.

As indicated in this graph, the lethal temperature of the bullhead rose from 29.1° C. on May 12 to 35.3° C. by July 8. From this peak it dropped back to 32.6° C. by September 11. The lethal temperature of the golden shiner rose from 30.3° C. on May 28 to a high of 33.4° C. on July 8, and fell back to 30.4° C. on September 8. On May 12 the creek chub had a lethal temperature of 28.2° C., on July 28, 32.6° C., and on September 7, 30.0° C. (tables 3, 4, 5).

Seasonal Variation for Lake Amikeus Fish

The three fish investigated from lake Amikeus were the fathead minnow, the redbelly dace, and the finescale dace. Since these fish came from a very shallow and exposed end of the lake and could all be seen at any time of the day swimming and feeding together in large numbers, it is reasonable to suppose that their thermal histories were almost identical and that any differences in their lethal temperatures were not complicated by possible differences in their habitat. The first determinations completed on May 9 revealed lethal temperatures of 29.0° C. for the fathead minnow, 29.7° C. for the redbelly dace, and 31.1° C. for the finescale dace. By July 5 these had risen to 34.0° C. for the fathead minnow, 32.8° C. for the redbelly dace, and 32.2° C. for the finescale dace, while by August 24 their lethal temperatures had dropped to 30.8° C., 31.1° C., and 31.2° C. respectively (figure 5; tables 6, 7, 8).

The most striking fact about these fish, unlike those from lake Opeongo, is the crossing over of their lethal temperature curves, first in the month of May and again at the end of August when the May temperature conditions were duplicated. This is in contrast to the parallelism exhibited by the other three species. Before May, 1941, the order of temperature resistance of these three minnows would place the fathead minnow at the bottom and the finescale dace at the top. By May their resist-

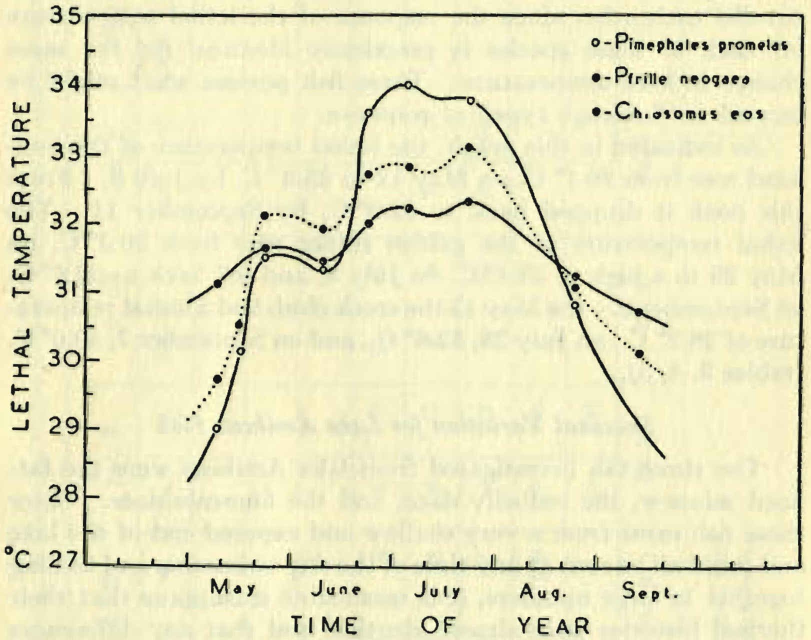

FIGURE 5.—Seasonal variation in the lethal temperature of three species from lake Amikeus, 1941.

ances had become approximately equal, while, one month later, the fathead minnow had risen far above the other two with the finescale dace now at the bottom of the tolerance order. Among the forms studied these two species of minnows, *Pimephales promelas* and *Pfrille neogaea*, represent the extremes in response of lethal temperature to a change in thermal environment. The fathead minnow shows a very wide range of adaptation, building up to a high level of temperature tolerance, while the finescale

TABLE 6.—Seasonal variation in the lethal temperature of *Pimephales promelas* (1941).

Date	May 9		May 16		May 23		June 10		June 23		July 5		July 23		Aug. 24	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
28	10	20	10	0												
29	15	66														
30	20	80	9	44	15	7										
31	20	100			15	47	18	50					10	0	12	42
32			8	100	12	58	21	91	12	8	22	14	10	0		
33					20	85	16	100	17	47	19	26	13	38	12	100
34					21	86	21	100	18	56	19	32	15	47		
35					13	100			14	79	15	60	12	92		
36											12	100	10	100		
Lethal Temperature	29.0		30.1		31.6		31.3		33.6		34.0		33.8		30.8	

T° C.—Temperature of experimental tank.
No.—Number of fish used in each tank.
%—Per cent mortality.

TABLE 7.—Seasonal variation in the lethal temperature of *Pfrille neogaea* (1941).

Date	May 9		May 23		June 10		June 23		July 5		July 23		Aug. 24		Sept. 13	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
29	9	0													15	7
30	9	0	10	0											15	40
31	14	36	10	0	8	63	10	0			10	0	8	0	6	100
32	8	100	19	74	9	100	9	44	19	32	11	27	8	50	15	100
33			15	100	9	100	13	100	9	100	12	100	10	100		
34							9	100	14	100	12	100	11	100		
Lethal Temperature	31.1		31.6		31.4		32.0		32.2		32.3		31.2		30.7	

T° C.—Temperature of experimental tank.
No.—Number of fish used in each tank.
%—Per cent mortality.

TABLE 8.—Seasonal variation in the lethal temperature of *Chrosomus eos* (1941).

Date	May 9		May 16		May 23		June 10		June 23		July 5		July 23		Aug. 24		Sept. 13	
T° C.	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
28	10	0																
29	8	13	10	0													15	13
30	8	38	13	61	10	0									10	0	15	40
31	7	100	10	80	10	0	14	36					10	0	40	37	15	100
32					17	29	15	47	11	27	15	27	10	0	36	95	15	100
33					12	100	16	100	14	36	25	74	28	40	32	100		
34					8	100	20	100	15	100	17	100	15	93				
35									11	100	16	100	10	100				
Lethal Temperature	29.7		30.5		32.1		31.9		32.7		32.8		33.1		31.1		30.1	

T° C.—Temperature of experimental tank.
No.—Number of fish used in each tank.
%—Per cent mortality.

dace illustrates a form in which the temperature tolerance remains comparatively high for all conditions, varying only slightly for large changes in lake temperature.

Here, as with the species from lake Opeongo, the dips and crests of the averaged lake temperatures were found to be reflected by similar changes of lesser magnitude in the seasonal variation of the lethal temperatures for each species.

UPPER AND LOWER LETHAL TEMPERATURE RELATIONS OF THE BULLHEAD

Since the upper lethal temperature of fishes may show comparatively smaller or greater degrees of variation for the full range of adaptation, it is impossible for comparative purposes to represent this index of temperature tolerance simply by a point. It must be extended to represent the complete relation of lethal and acclimation temperatures, that is, it must be extended from a point to a line and thus cover the whole field (figure 6).

For experiments concerning the relation of the lethal temperature and acclimation temperature, it is necessary to keep the fish at constant temperatures until, with the completion of acclimation, the lethal temperature becomes constant. Lethal temperature determinations are then carried out in exactly the same manner as described.

A series of experiments on the relation of the lethal temperature to the acclimation temperature, similar to those described for young goldfish (Fry *et al.*, 1942), were performed for the bullhead. Groups of forty fish were acclimated to 6° C., 13° C., 20° C., 26° C., 31.2° C., and 36° C. respectively and their upper lethal temperatures determined for each of these acclimation temperatures (table 9). In general, the time for acclimation was set at one day for each change of 1° C. At the lowest level, 6° C., the time spent in acclimation was extended, three months being spent in bringing the fish down from 20° C. to this level.

In addition to these, a series of lower lethal temperature experiments on the bullhead was completed for different states of temperature acclimation. In this series the level of acclimation was raised from 21° C. by 2° C. every second day and the lower

lethal temperatures established for acclimation temperatures of 25° C., 30° C., and 36° C. (table 10). The procedure used in determining the lower lethal temperature is described in a later section (p. 41).

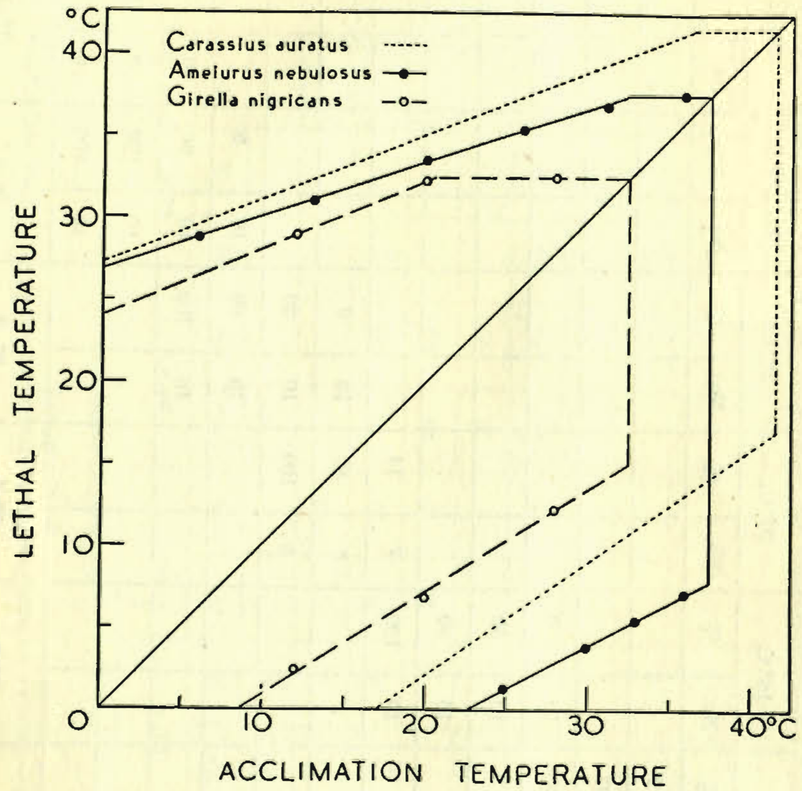

FIGURE 6.—The relation between the acclimation temperature and the upper and lower lethal temperatures for *Carassius auratus*, *Ameiurus nebulosus*, and *Girella nigricans*.

RANGE OF THERMAL TOLERANCE OF THE BULLHEAD

The completion of experiments on low lethal temperatures for the bullhead terminated the study of the whole range of thermal tolerance for this species. A similar study has been pub-

TABLE 9.—Relation between upper lethal temperature and acclimation temperature of the bullhead.

T° C.	Acclimation temperature 6° C. No.	%	13° C. No.	%	20° C. No.	%	26° C. No.	%	31.2° C. No.	%	36° C. No.	%
28	7	0										
29.5	8	87										
30	8	100	10	0								
31			10	50								
32			10	90								
33			10	100	7	14						
34					8	87	10	0				
35					8	100	10	30				
36							10	90	10	0		
37							10	100	10	60	10	0
38									10	100	10	100
39									10	100	10	100
Lethal Temperature	28.9		31.0		33.4		35.3		36.9		37.5	

T° C.—Temperature of experimental tank. No.—Number of fish per tank. %—*Per cent mortality.*

TABLE 10.—Relation between lower lethal temperature and acclimation temperature of the bullhead.

T° C.	Acclimation temperature 21° C. No.	%	25° C. No.	%	30° C. No.	%	33° C. No.	%	36° C. No.	%
0.4	10	10								
1.2	10	0	12	50						
2.0	10	0	10	20	10	100				
3.0			10	0	10	80				
4.0					10	40				
5.0					10	10	10	70		
6.0					10	0	10	20		
7.0							10	0	10	50
Lethal Temperature	-1.0		1.3		3.7		5.3		7.0	

T° C.—Temperature of experimental tank. No.—Number of fish per tank. %—Per cent mortality.

lished by Fry *et al.* (1942) for the goldfish, the data from which have been plotted in figure 6 for comparison with those of the bullhead. As pointed out in the case of the young goldfish, a trapezium may be constructed which no longer expresses the temperature tolerance in terms of points but as an area bounded above and below by the lines relating the upper and lower lethal temperatures to the acclimation temperature, and laterally, by two perpendiculars, one erected at the 0° C. acclimation point and the other at that temperature of acclimation which is equal to the upper lethal temperature. In figure 6 the trapezium for the thermal tolerance of bullheads is shown in solid black lines while that for the goldfish is dotted.

In his paper, "The Resistance and Acclimation of Marine Fishes to Temperature," Doudoroff (1942) includes experiments on the upper and lower lethal temperatures of *Girella nigricans*, the greenfish, for a number of different acclimation temperatures. The liberty has been taken to plot these results in the manner of those for the bullhead and the goldfish. Thus, the central trapezium in figure 6 (broken line) is that for the greenfish, a marine fish from the coastal region of California and not exposed to the more extensive variations of temperature experienced in an area as far north as Algonquin Park.

To quote from "The Lethal Limits of Temperature for Young Goldfish" (Fry *et al.*, 1942): "the thermal tolerance which the area (of the trapezium) represents allows the degree of eurythermicity of the organism to be expressed quantitatively. The problem of dealing with the lower lethals below 0° C. in the case of a freshwater fish is a vexing one. This difficulty may be put aside for the time being by considering it to be a region outside that in which the animal can be active. As a minimum description the goldfish might be said to have an ultimate upper lethal temperature of 41° C., an ultimate lower lethal of less than 0° C. and a thermal tolerance of 1,220 units in the zone of temperatures in which it can be active." In this case the "1,220 units" are units of "degrees centigrade squared" and represent the area bounded by the dotted lines for the goldfish in figure 6. By expressing this area in degrees centigrade squared, a convenient index of comparison of eurythermicity for different species of fish

is presented. For the bullhead the thermal tolerance is 1,162 units, not much less than that for the goldfish. The greenfish, however, has a thermal tolerance of some 800 units which is about three-fifths of that for the goldfish.

For acclimation temperatures from 0° C. to 33° C. the relation is linear for the upper lethal temperature of the bullhead, after which the upper lethal temperature, which has a steady rise from 27° C. at the rate of about 1° C. for every 3° C. rise in acclimation temperature, levels off and does not exceed 37.5° C. From the results of experiments with goldfish, a definite break in the straight-line relation of the lethal temperature to the acclimation temperature apparently occurs at the higher levels of acclimation. In this region, although the acclimation temperature may still be raised, no change in the lethal temperature results. The same break occurred in the case of the bullhead and is apparently also present in the greenfish.

The gradient of the lower lethal temperature relative to the acclimation temperatue is somewhat sharper than that for the upper lethal temperature. It changes by 1° C. for every change of 2° C. of acclimation, extending from a lethal level of 0° C. at 22.5° C. acclimation to 7° C. at 36° C. acclimation.

The diagonal extending from the lower left-hand corner to the upper right-hand corner in this figure passes through all points where the acclimation temperature equals the lethal temperature. Wherever the upper lethal temperature line, for a given species, meets this diagonal line, there the ultimate upper temperature tolerance for that species has been reached and further temperature acclimation is impossible. This end point for the three species represented was 41.0° C. for the goldfish, 37.5° C. for the bullhead, and 32.5° C. for the greenfish.

RATE OF ACCLIMATION

As well as demonstrating variations in the lethal temperature with change of acclimation temperature, the papers of both Loeb and Wasteneys (1912), and Sumner and Doudoroff (1938), include data on the rate of adaptation of fish to high temperatures. The greater part of the adaptation for an upward change of acclimation temperature of 10° C. (range of 20° C. to 30° C.) was found to be complete within twenty-four hours for the long-jawed goby, *Gillichthys mirabilis*. A more extensive study of this problem has recently been published by Doudoroff (1942) in which the results of experiments concerning the adaptation of young greenfish, *Girella nigricans*, to both high and low temperatures are presented.

The method employed in this investigation for following the rate of acclimation was that originally used by Loeb and Wasteneys (1912). This is done by tracing the change in the average rate of mortality at a given high temperature until no change in the rate is obtained. This method provides a measure of the rate of change in tolerance to a high temperature and is therefore a measure of acclimation only in this respect.

The primary investigation concerned the rate of acclimation of *Pimephales promelas* to a low temperature. This species of minnow was chosen because of its abundance and its hardiness in captivity. One hundred and ninety-five fish were trapped on August 1 when the lake temperature was 24° C. and transported to a fifteen-gallon tank at the laboratory. The temperature of the water in the tank was maintained at 16.0 ± 0.5° C. for twenty-two days, the duration of the experiment. The tank was imbedded in sawdust in a specially constructed insulated bin and the temperature kept down by crushed ice. From the lethal temperature curve for a sample of these fish taken straight from the lake, the critical temperature was found to be 32.6° C., representing that temperature at the very top of the survival curve where mortality, if present, is very low. For fish conditioned to 16.0° C. this temperature appears at the bottom of the curve where the average mortality time is of short duration. The rate of acclimation was followed by determining the average time of mortality at 32.6° C. for samples of fifteen fish taken at various time intervals from the tank.

The progress of this temperature adaptation is plotted in figure 7 and appears as a sigmoid curve tapering off slowly with the approach of complete acclimation. For the first two and one-half days the average mortality time showed no change. By the fifth day the mortality time had dropped from twelve to eleven hours and continued to drop right down to a little over

one hour by the thirteenth day. Ten fish remained and these were allowed to go for twenty-two days at which time the mortality rate at 32.6° C. was found to be very high, the average time to die being approximately ten minutes and about equal to that for fish completely acclimated to a temperature of 16° C. Fifty per cent of the acclimation had taken place within seven and one-half days and by the thirteenth day nearly ninety per cent acclimation had occurred.

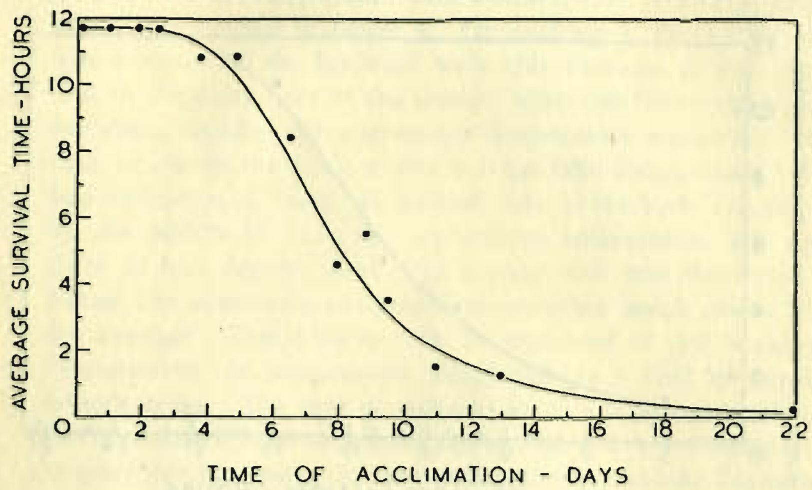

FIGURE 7.—The average survival time at 32.6° C. of *Pimephales promelas* when taken from 24° C. and put at 16° C.

In contrast to this relatively slow loss of resistance to a high temperature when colder thermal conditions are experienced, the rate of adaptation to an environment of higher temperature is very much faster and may take place in a matter of hours rather than days. This latter rate of acclimation was determined for the bullhead using the same method of following the rate of mortality at a given temperature as an index of the extent of adaptation. In this case fish from water of 20° C. were put at 28° C. and the average mortality time at 35.5° C. followed for twenty-four hours. From the curve plotted in figure 8 it will be seen that the average mortality time for ten fish climbed from forty-five minutes at the start of the experiment to just under twelve hours by the end of twenty-four hours and equivalent to the mortality time of bullheads acclimated to 28° C.

In the experiments which involved acclimation of fish to progressively higher temperatures, the rate of change used was 1° C. per day which would appear from the foregoing experiments to be well beyond the necessary limits for ensuring complete acclimation.

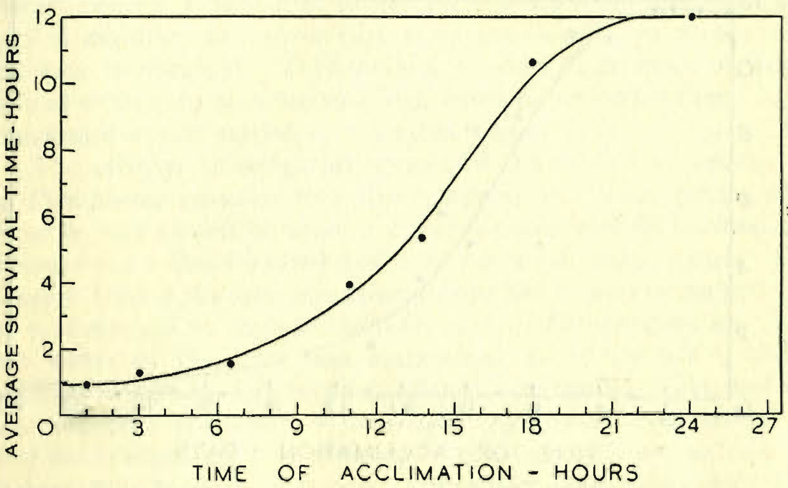

FIGURE 8.—The average survival time at 35.5° C. of *Ameiurus nebulosus* when taken from 20° C. and put at 28° C.

SUMMATION IN ACCLIMATION

The relation of the lethal temperature to the acclimation temperature, established for the upper and lower limits of temperature tolerance for the bullhead, provided a means of determining the acclimation temperatures of the bullheads which underwent lethal temperature determinations in the study of seasonal variation. For example, the upper lethal temperature of the bullhead, on June 14, 1941, from lake Opeongo was 33.2° C. For this lethal temperature, by use of the graph in figure 6, it will be seen that the corresponding acclimation temperature is

20° C. In a similar manner, for each of the twelve upper lethal temperatures of the bullhead determined during the study of seasonal variation (figure 4) the corresponding acclimation temperatures can be obtained. These latter, collectively, provide the actual changes which occurred in the thermal adaptation of the species.

As was stated previously, the maximum and minimum temperatures of the lake water were averaged and it is this average which was plotted in figure 4. On comparing the acclimation temperatures of the bullhead with this average, it was found that in the early part of the season, when the lake temperature was rising rapidly, the acclimation temperature was either lower than or almost the same as the average lake temperature. The approximation of these two existed only in the early stages and by the middle of June the acclimation temperature had risen three to four degrees above the average and was discovered to follow the maximum temperatures recorded much closer than the average. This relation may be explained on the basis of a "summation" in temperature adaptation in a field of varying temperatures. The rate of acclimation to a higher temperature has been shown to be very much faster than the rate of adaptation to a low temperature. As the temperature in the lake fluctuates, each new height raises the temperature adaptation by a corresponding increment which is not lost with the nightly fall in temperature or with cold spells of short duration. In this way a type of "summation" occurs in which the acclimation temperature is not a function of the average water temperature, but is closer to the maxima recorded for that period of time during which the lake temperature is rising toward the highest peak of the year. As the temperature steadily falls from this peak, with the approach of winter conditions, the acclimation temperature remains considerably above even the maximum because of the slow loss of adaptation to the higher temperatures. Figure 9 has been included to illustrate this relation between the acclimation temperature and the maximum and average lake temperatures.

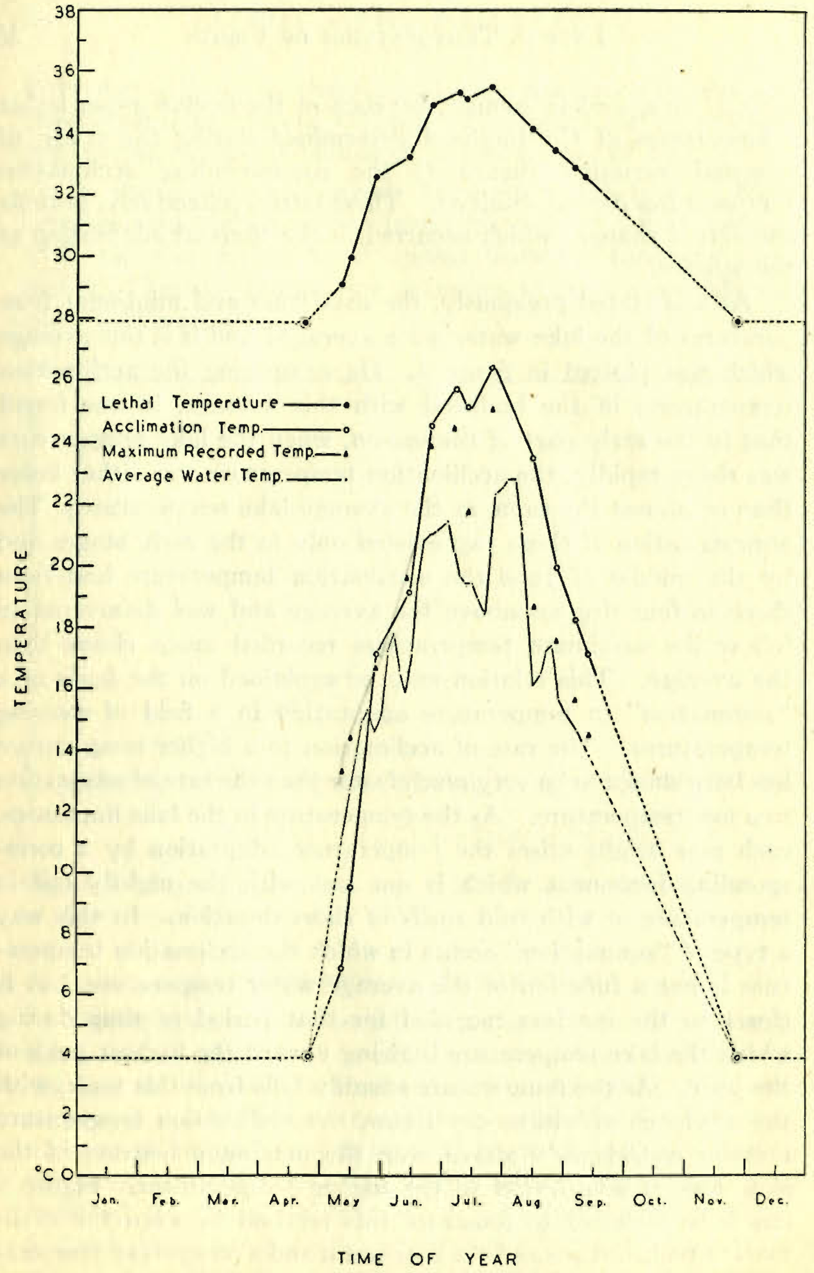

FIGURE 9.—The relation of the lethal temperature and corresponding acclimation temperature of *Ameiurus nebulous* to the maximum and average lake temperatures in lake Opeongo.

COMPARATIVE UPPER LETHAL TEMPERATURES

A period when the temperature conditions reached a maximum and in which they remained fairly constant occurred at the end

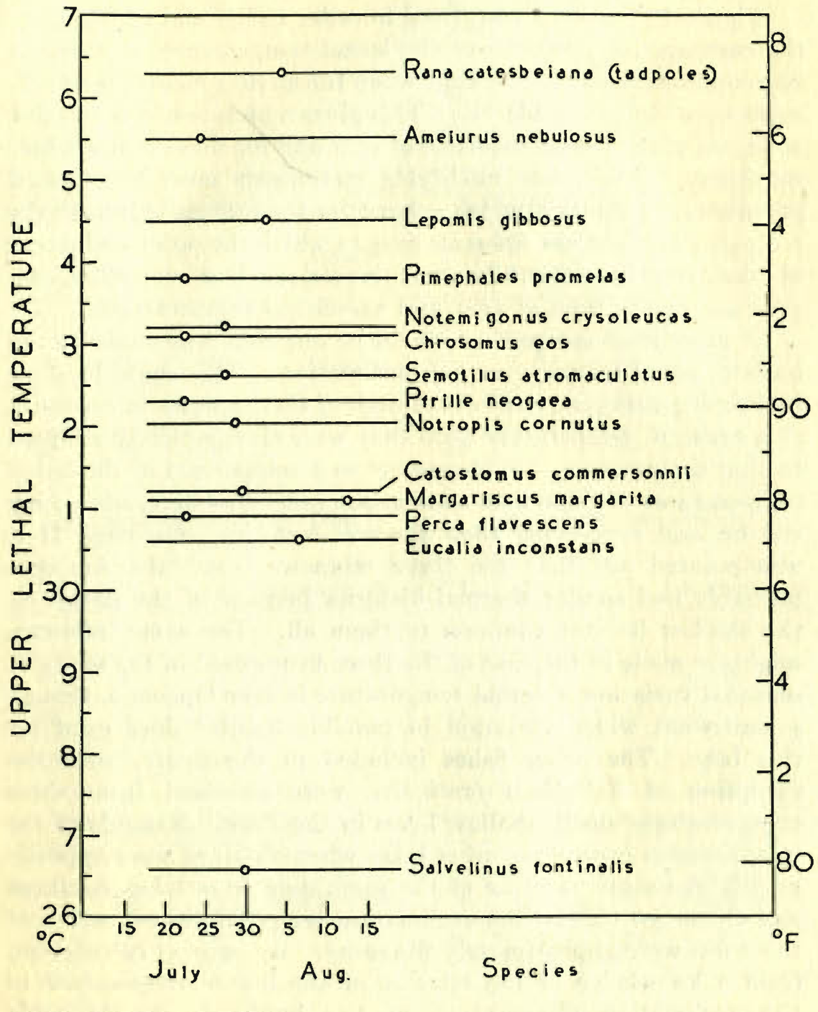

FIGURE 10.—Upper lethal temperatures of thirteen species of fish from Algonquin Park. The *x*-axis indicates the date of each lethal temperature determination.

of July and during the first week of August 1941. Every effort was made to carry out lethal temperature determinations at this time on as many species as could be obtained in sufficient numbers.

Figure 10 has been composed in order to list and to illustrate the comparative positions of the lethal temperatures of thirteen Algonquin Park fish at the time when the environmental temperatures were highest (table 11). This gives a picture of the relative positions of the fish at this time of year and for these temperature conditions. The latter modifying statements must be stressed in view of the relation which existed for the fathead minnow, the redbelly dace, and the finescale dace in which the order andextent of their temperature tolerance showed such a variation, depending on the time of year and associated temperatures.

A more ideal comparison would be one that was made on the basis of equal temperatures of acclimation. This could be done by keeping sufficient numbers of each of these species in captivity at a constant temperature until they were all completely adapted to that temperature. With respect to a comparison of the lethal temperatures of these fish, as they are presented here, something can be said concerning their thermal histories. On page 21 it was pointed out that the three minnows from lake Amikeus probably had similar thermal histories because of the nature of the shallow habitat common to them all. The same inference might be made in the case of the three fishes used in the study of seasonal variation of lethal temperature in lake Opeongo, though a somewhat wider variation in possible habitat does exist for this lake. The other fishes included in the figure, with the exception of *Salvelinus fontinalis*, were obtained from three comparatively small, shallow lakes in the Park. Records of the temperatures from these other lakes when obtained were approximately the same as those of the same date from lakes Amikeus and Opeongo. Thus, the acclimation temperatures of twelve of these fish were approximately the same. By indirect calculation, from a knowledge of the relation of the lethal temperature to the acclimation temperature in the bullhead, the probable temperature of acclimation for these twelve fish was in the region of 25° C. to 26° C.

TABLE 11.—Comparative upper lethal temperatures

Perca flavescens—July 23				*Notropus cornutus*—July 29			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
30	8	13		30	6	0	
31	9	33	30.9	31	6	17	32.0
32	9	100		32	6	67	
33	7	100		33	6	100	
Margariscus margarita—Aug. 13				*Eucalia inconstans*—Aug. 7			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
30	8	0		30	7	14	
31	8	37	31.1	31	7	86	30.6
32	9	100		32	6	100	
33	8	100		33	7	100	
Catostomus commersonnii—Aug. 1				*Lepomis gibbosus*—Aug. 3			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
30	7	14		33	7	0	
31	8	37	31.2	34	8	37	34.5
32	8	100		35	8	63	
33	7	100		36	6	100	
Salvelinus fontinalis—June 20				*Rana catesbeiana* tadpoles—Aug. 5			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
26	7	43		36	5	20	
27	7	100	26.1	37	9	89	36.3
28	7	100		38	5	100	

T° C.—Temperature of experimental tank.
No.—Number of fish per tank.
%—Per cent mortality.

In figure 10 at the very top appears a point for bullfrog tadpoles (*Rana catesbeiana*) indicating the high tolerance of this aquatic larval amphibian. Additional experiments on this species showed it to be a very tolerant form with a lethal temperature which varied with changing thermal conditions as in the case of the fish.

At the very bottom of the list a point for speckled trout appears. The date for this determination was June 20, but the liberty has been taken to include it in this table since the temperature of the stream from which these fish were caught was then approximately at its maximum for the year.

COMPARATIVE LOWER LETHAL TEMPERATURES

There are several references in the literature of death among poikilotherms as a result of chilling from temperatures above the freezing point of water (Storey, 1937; Storey and Gudger, 1936). Verrill (1901) reports the death of many species of fish after a rather severe winter in Bermuda and yet the coldest temperature recorded was not lower than 7° C. Other factors may have played a part in this instance but the fact remains that it does not require temperatures of 0° C. and below to cause death in fishes. On the other hand, both Britton (1924) and Luyet (1938) have demonstrated the survival of some species of fish at temperatures below the freezing point of their body fluids. The present consideration deals only with temperatures above 0° C., a field of investigation which has received little attention by other workers except Fry *et al.* (1942) and Doudoroff (1942).

On exposing fish to water of a temperature low enough to cause some mortality, yet above 0° C., the first reaction is one of great activity which is quickly followed by an obvious numbing and general cessation of muscular contraction interspersed with sudden bursts of activity. Almost from the start respiratory movements cease and progressive loss of equilibrium takes place. Within ten minutes all the fish are completely overcome and, unless stimulated, give no outward indication of vital activity. For a given stimulus the response slowly falls off until none can be obtained, even for a strong touch stimulus. If the fish are then placed in a water bath of higher temperature they will quickly recover and present a normal appearance. It was for this reason that definite criteria of "living" and "dead" had to be established. Among those fish which are destined to live at temperatures low enough to cause mortality in others, a small amount of activity may be observed by the end of ten to twelve hours which develops to a state of slow but continuous activity of both respiratory and general body movements by twenty-four hours. Most of the experiments did not last for more than twelve hours so that little can be said concerning the effect of prolonged low temperatures.

The index used for the low lethal temperature was that temperature from which, after a period of twelve hours, only fifty per cent of the fish recover. This serves as a definition. In practice, at the end of the twelve-hour period in the cold tanks the fish were all removed and put into a water bath of a medium non-lethal temperature. Certain fish will obviously be living after twelve hours from the activity they exhibit while still at the low temperature, but there is some difficulty in determining this fact for others, while still others appear to be quite dead. In order to distinguish the exact extent of mortality, any fish that showed signs of recovery (respiratory movements, muscle contraction) after one hour at the medium temperature were grouped as "living," the remainder as "dead." Since the range of low temperatures over which all the fish were either completely dead or completely living was not great, the above method was adopted as an adequate and standard means of recording the intermediate points. The condition of the fish after twelve hours at a temperature one or two degrees above a critical low temperature was one of healthy activity with no visible impairment, which would indicate that the above system provided a good criterion for the lower lethal temperatures.

During the period of highest lake temperature conditions, about the middle of August with an average of 21° C., the low lethal temperatures were determined for eight species of fish (table 12) and appear in figure 11 arranged in order of the least tolerant to the most tolerant. The lethal temperatures recorded below 0° C. have been obtained by extrapolation from the mortality curves. This may be taking unwarranted liberties as no

TABLE 12.—Comparative lower lethal temperatures

Ameiurus nebulosus				*Margariscus margarita*			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
0.3	10	10		0.3	8	25	
1.3	10	0	-0.8	1.3	10	0	-0.2
2.0	10	0		2.0	5	0	

Pfrille neogaea				*Semotilus atromaculatus*			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
0.3	10	90		0.3	11	92	
1.3	22	50	1.3	1.3	8	63	1.7
2.0	10	10		2.0	9	44	
2.8	20	5		2.8	11	8	

Pimephales promelas				*Chrosomus eos*			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
0.3	15	100		0.3	17	100	
1.3	24	70		1.3	20	100	
2.0	13	62	2.1	2.0	31	77	2.7
2.8	18	28		2.8	21	45	
				4.2	10	0	

Perca flavescens				*Notemigonus crysoleucas*			
T° C.	No.	%	Lethal temperature	T° C.	No.	%	Lethal temperature
1.3	5	100		1.3	6	100	
2.0	4	100	3.1	2.0	10	100	3.4
2.8	10	60		2.8	10	70	
4.2	12	0		4.2	6	0	

T° C.—Temperature of experimental tank.
No.—Number of fish per tank.
%—Per cent mortality.

experiments below 0° C. were performed. However, since the mortality of bullheads is so low at 0.5° C. and in view of the fact that other experimenters have demonstrated the existence of fish at temperatures below 0° C., it seems probable that the low

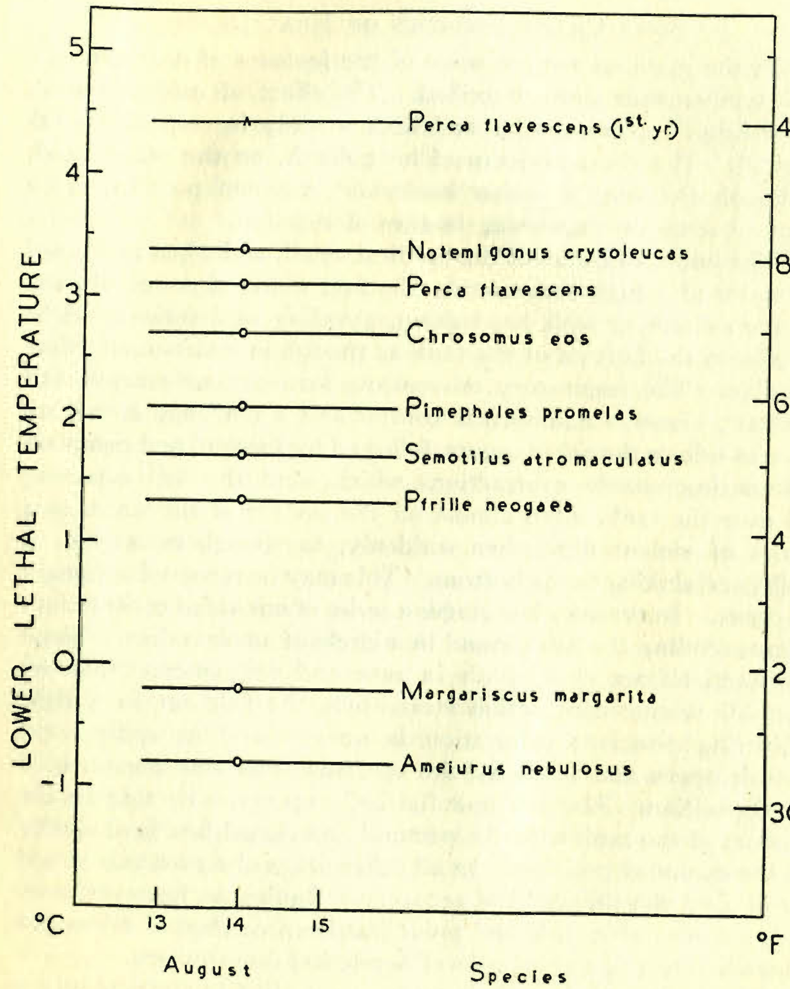

FIGURE 11.—Lower lethal temperatures of eight species of fish from Algonquin Park. The *x*-axis indicates the date of each lethal temperature determination. Peliminary experimerts showed that the lethal for first year *P. flavescens* was 4.5° C. or higher as indicated by the inverted "V."

lethal temperature for the bullhead is in the region of -1° C. for this state of acclimation. There is also nothing unusual or disorderly about the change of low lethal temperature with acclimation temperature as 0° C. is approached.

SOME CHARACTERISTICS OF HEAT DEATH

In the previous section some of the features of death from a low temperature were described. The effect of cold water on most fishes is very similar and little variety in response is exhibited. The characteristics of heat death, on the other hand, although following a rather basic and common pattern, often contain some distinguishing feature of reaction.

The bullhead is one of the hardiest of all, and when immersed in water of a high temperature the first reaction is one of very active swimming with head down, gyrating in a series of tight circles on the bottom of the tank as though in a strenuous effort to dive. The respiratory movements are extremely rapid and shallow. Loss of equilibrium control and a tendency to roll up on one side or the other occurs, followed by forceful and complete alternating muscle contractions which send the fish careering all over the tank, often almost off the surface of the water in a series of violent flips, then suddenly, as though exhausted, it collapses, sinking to the bottom. This may be repeated a number of times. In the very last stages a series of one-sided contractions occur, sending the fish around in a circle of small radius. These contractions are slow, both in rate and frequency. Soon an over-all tetanic contraction straightens the fish out in a rigid quivering position; respiration is uneven and in spurts; the mouth opens and in many the opercula arch and remain in a fixed position. The fish now lies belly up or on its side on the bottom of the tank with the pectoral and dorsal fins fixed rigidly in the extended position. In all other fishes observed this would be beyond the threshold of recovery. Bullheads, however, may recover even after this end point has been reached if taken out immediately and put at a lower non-lethal temperature.

The bullheads pass their refuse soon after immersion in the high-temperature tank and many regurgitate partially digested food. Colour changes are frequent. The usual intense black

of the dorsal surface of the bullhead often becomes blotched with light areas of a green yellow. The black may become distinctly purple with varying patterns of irregular hues involving green, yellow, and purple. In other species such variety of colour change was not observed.

The creek chub, like the fathead minnow, is deceptive in its reaction to a high temperature. For any sudden rise in temperature of about 8° C. to 10° C., although some degrees below the lethal level, it gives every indication of the onset of heat death, even to the point of floating belly-up on the surface of the water. Despite this, after a short time and once accustomed to the new conditions the fish will live and give no further indication of the apparent approach of death. At a lethal temperature these fish usually swim around belly-up at the surface exhibiting complete loss of equilibrium. The last stages of death are characterized by a series of contortions and amazing activity with such strength of muscular contraction that the spinal column may be completely twisted out of shape or arched with the caudal fin almost touching the head. After death the fish float upside down at the surface, whereas the bullheads are usually found to have sunk to the bottom.

The pearl dace is very similar to the chub in its response to a high lethal temperature but is often distinguished by the arching out of the pectoral fins in a rigid fan-like extension. Another species, the common shiner, is also very similar in its characteristics of heat death to those of the chub and pearl dace. The golden shiner, however, continues to respire at a rapid rate long after all other muscular contractions have stopped. Finally these movements also cease and the fish floats to the surface. In contrast to this last species, the respiratory movements of the yellow perch are inhibited completely with the approach of heat death. The mouth opens wide and the opercula fan out spreading the gills apart in a fixed position. Although the fish may swim around for some time renewing the oxygen supply to the gills, no movement of the opercula or gills occurs and death eventually overcomes the fish.

One feature of heat death characterizes only the male finescale dace and some redbelly dace, which show a spreading of the pectoral fins in a permanent fixed position not long before death.

DISCUSSION

In this study of lethal temperature relations of some of the species of fish from lakes in Algonquin Park it can be concluded that the lethal temperatures of the species investigated are fine yet flexible end-points which show distinct variations during the course of the year and which are directly related to the variations in temperature of the lake water from which the species were obtained. This correlation gives an excellent indication of the extensive adaptive powers of freshwater fish and the great variation in the lethal temperature which rises and falls with ascending and descending lake temperatures.

A type of "summation" in adaptation exists for the majority of species which enables them to maintain a temperature tolerance which builds up high enough to be sufficient to resist the heights of temperature which occur in their environment during the hottest season of the year. *Pimephales promelas* proved to have the greatest adaptive powers while *Pfrille neogaea* had the least, yet this latter species was sufficiently resistant to overcome all temperature heights reached in a shallow exposed lake. Among those with an "average response" to temperature change *Ameiurus nebulosus* was the hardiest of all.

A knowledge of the acclimation temperature is of prime importance when determining the lethal temperature, without which any statement of the lethal temperature is practically useless from a comparative standpoint. The full significance of this is revealed by the relationship which exists between these two for *Ameiurus nebulosus*. To state that the lethal temperature of this species, is 27.5° C. is just as valid as recording it at 37.5° C. provided the relative states of temperature acclimation are also included. A complete description of the temperature relations for fish is best obtained by the method originally described for the goldfish, *Carassius auratus*, where a trapezium was constructed relating the lethal and acclimation temperatures for water of 0° C. and above. To this has been added the trapezium of temperature tolerance for *Ameiurus nebulosus*.

The experiments concerning lower lethal temperatures demonstrated that temperatures above 0° C. may be lethal for fish taken directly from natural conditions even in species which spend the winter under a cover of ice, and that an adaptation must take place to low as well as to high temperatures for fish inhabiting freshwater regions where the lakes freeze over at some time during the year. A menace from both extremes of temperature therefore exists. Since adaptation to lower temperatures proceeds at a rate very much slower than that for higher temperatures, the possibility of death from a low temperature in nature may well be greater than that from high temperatures.

The results on the rate of acclimation to a high temperature showed that a rapid rate of adaptation exists for *Ameiurus nebulosus* which is probably typical of most species and confirms the results obtained by other workers in this field. This rapid acclimation is reflected in an ability to keep pace with the fast-changing lake-water temperatures which rise with such speed in the early part of the summer. Two factors must therefore be in operation limiting the distribution of less tolerant fish from the standpoint of temperature conditions, the upper and lower limits of temperature tolerance and the rate of acclimation to these extremes.

SUMMARY

Since the fish in the lakes of Algonquin Park, Ontario, are exposed to wide variations in temperature throughout the course of a year, experiments were performed to determine if changes in the lethal temperature of some of these species occurred during the period of greatest temperature change in the lake water. Most of the work was concerned with the upper lethal temperature which was defined as that temperature at which fifty per cent of the fish die if exposed for a period of twelve hours.

The changes in the upper lethal temperatures of the bullhead, the golden shiner, and the creek chub, caught from lake Opeongo, and of the finescale dace, the redbelly dace, and the fathead minnow, caught from lake Amikeus, were obtained for the late spring and summer months. These were studied in relation to the changes in lake-water temperature for that period of time.

The lethal temperature of the bullhead rose from 29.1° C.

on May 12 to 35.3° C. by July 8, while that of the finescale dace for approximately the same period of time, only varied from 31.1° C. on May 9 to 32.2° C. by July 5. The changes in lethal temperature throughout the study of each of the six species reflected the major changes in water temperature, rising with ascending lake temperatures and falling as the temperature of the water fell with the approach of winter conditions.

The complete range of thermal tolerance of the bullhead, comprising the relation of both the upper and lower lethal temperatures to changes in acclimation temperature from 6° C. to 36° C. (figure 6), has been determined and compared with the results from similar experiments on the goldfish (Fry *et al.*, 1942). The thermal tolerance in degrees centigrade squared was found to be 1,162 units, not much less than that for the goldfish, while the ultimate upper lethal temperature was 37.5° C.

Starvation in bullheads for forty days at summer temperatures had no appreciable effect on the upper lethal temperature.

Two experiments on the rate of acclimation were performed. The first was on the rate of acclimation of the fathead minnow to 16° C. when taken from water of 24° C. No change in temperature resistance was obtained for the first two and one-half days after which time the resistance gradually fell off, reaching a new level at the end of about twenty days. The second experiment dealt with the rate of acclimation of the bullhead to a temperature of 28° C. when taken from that of 20° C. In this case the temperature resistance rose to that for 28° C. within twenty-four hours.

In addition to the six species used in the study of seasonal variation in lethal temperature, the upper lethal temperatures for seven other species of fish, determined when the lake-water temperatures were approximately at their highest peak for the year, are presented (figure 10), as well as the lower lethal temperatures for eight of this total number (figure 11), also obtained at that time.

Some of the characteristics of heat death are described for most of the species subjected to lethal temperature experiments.

LITERATURE CITED

BELEHRADEK, J. 1935. Temperature and living matter. Protoplasma-Monographien, vol. 8. Berlin. 229 pp.

BRETT, J. R. 1941. Tempering versus acclimation in the planting of speckled trout. Trans. Amer. Fish. Soc., vol. 70, 397-403.

BRITTON, S. W. 1924. The effects of extreme temperatures on fishes. Amer. Jour. Physiol., vol. 67, 411-421.

DOUDOROFF, P. 1942. The resistance and acclimatization of marine fishes to temperature changes. I. Experiments with *Girella nigricans* (Ayres). Biol. Bull., vol. 83, 219-244.

FRY, F. E. J., J. R. BRETT and G. H. CLAWSON. 1942. Lethal limits of temperature for young goldfish. Rev. Can. de Biol., vol. 1, 50-56.

HATHAWAY, E. S. 1927. Quantitative study of the changes produced by acclimation on the tolerance of high temperatures by fishes and amphibians. Bull. U.S.B.F., vol. 43, part 2, 169-192.

HEILBRUNN, L. V. 1937. An outline of general physiology. Philadelphia. 603 pp.

HUBBS, C. L. and K. F. LAGLER. 1941. Guide to the fishes of the Great Lakes and tributary waters. Michigan. 100 pp.

LOEB, J. and H. WASTENEYS. 1912. On the adaptation of fish (*Fundulus*) to higher temperatures. Jour. Exp. Zool., vol. 12, 543-557.

LUYET, B. 1938. Sur la survie des poissons plongés dans l'air liquide. C.R. Soc. Biol., vol. 127, 788-790.

STOREY, M. 1937. The relation between normal range and mortality of fishes due to cold at Sanibel Island, Florida. Ecology, vol. 18, 10-26.

——— and E. W. GUDGER. 1936. Mortality of fishes due to cold at Sanibel Island, Florida, 1886-1936. Ecology, vol. 7, 640-648.

SUMNER, F. B. and P. DOUDOROFF. 1938. Some experiments upon temperature acclimatization and respiratory metabolism in fishes. Biol. Bull., vol. 74, 403-429.

VERRILL, A. E. 1901. A remarkable instance of the death of fishes at Bermuda in 1901. Amer. Jour. Sci., series 4, vol. 12, 88-95.