RESISTANCE AND REACTIONS OF FISHES TO TEMPERATURE

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The relation of fishes to temperature has been a subject for considerable experimental and observational study in the past. The experimental work has dealt largely with the resistance of fishes to extremes of temperature, while numerous observations have been made both upon the resistance and the reactions of fishes to various temperatures. In 1853 Dr. John Davy experimented upon the resistance of a number of species of fishes to high temperatures, and in 1882, as recorded in Day's (1886) review of his work, Davy reported a considerable number of experiments upon the extremes of high temperature which eggs, fry, and adults of different species can stand without being killed. He found the egg to be more resistant to high temperatures than was the young fish and probably also than the adult. At 85° F. (29.4° C.) both the young and the old fishes were dead while the eggs still lived to hatch into normal, vigorous larvae. These results are not entirely satisfactory however, for one experiment is stated to have been performed upon the eggs, young, and adult of a given species under similar conditions. Day (1886) observed fish in the government garden in Madras, where, in December 1866, he found the maximum daily temperature of the water to be 72° F. (22.2° C.) He states that the Indian carp thrives in the lower rivers where the temperature at mid-day rises to 92° F. (33.3° C.) Carter (1887) gives a table of fishes which are sensitive or hardy in warm waters. He includes both marine and fresh water species giving the average maximum temperatures which species from the two habitats can stand. These maximum temperatures do not differ much for the two habitats being 50°-71° F. (14.4°-21.6° C.) for the fresh water species mentioned and 58°-71° F. (14.4°-21.6°C.) for those from salt water.

There are recorded cases where fishes are reported to have inhabited much higher temperatures, but most of these records are not well authenticated. Such cases will be found in the literature cited. There are also many records of fishes having endured low temperatures without injury. Many of these records are common knowledge and must be taken for what they are worth. There are, however, some definite experiments upon the relation of fishes to low temperature. Heath in 1883 tells of freezing several species of fishes in solid blocks of ice. He found that species thus frozen would regain their normal activities upon slow thawing. Other species were not so resistant, while all the species he tried died if kept in the frozen condition for more than a few hours. Pictet (1893) reports a number of experiments of the same sort. He kept gold fish at 0° C. for 24 hrs., and then slowly cooled the water to -8° to -15° C. The fishes were frozen solid and were as brittle as the ice. Upon thawing they became normal again and swam about the pan as before. When cooled to below -20° C. they could not be revived.

Much of the value of such data as the above is lost because of the failure of the workers to give specific names and accurate reports of temperatures and other experimental conditions. Thus there are numerous observations and speculations upon the influence of temperature upon the movements of fishes. Baird (1886) states that temperature is important in influencing the migrations of fishes and Verrill, according to Bumpus (1898) says the sudden death of the enormous numbers of "tile fish" in the year 1879 was probably due to a sudden lowering of the temperature of the waters usually warmed by the gulf stream. In 1899 Libbey began a series of observations to ascertain the connection between changes in temperature and the migrations of fishes. This investigation was merely a continuation of former investigations in which he had determined pretty definitely that movements of ocean currents and other changes in ocean temperatures are of very great importance in these migrations, (Bumpus '98). It is a matter of common observation among fishermen that certain fishes, for instance suckers, when they ascend the small streams in the spring to spawn, often seem to congregate in the warmer streams when there are numerous small streams of different temperatures to choose from.

PRESENTATION OF DATA

In the experiments to be briefly reported here, I have used the fresh water fishes of the creeks in the vicinity of Chicago and have performed with them two types of experiments, namely, resistance experiments and reaction experiments.

1. *Resistance Experiments*: These experiments have been of two sub-types. (1) Resistance to slowly changing temperatures, and (2) Resistance to suddenly changing temperatures. In the first sub-type the fishes were placed in a granite pan in about a liter of water (the species used have been small except in the case of the bull-head, in which case individuals not more than 4 in. long were used), at normal optimum temperature and the water was then heated gradually. The rate of heating was varied considerably in different experiments (5 min. up to 1 hr.) In killing experiments the heating was continued up to the point where death occurred; in other experiments the fish was taken out before the death point was reached.

As the water was being heated, the fishes gave very similar reactions, specific differences being quantitative rather than qualitative. At the beginning, the fish in the experiment swam about exactly as did the one in the control. As the experimental temperature increased, however, the activity of the experimental fish increased likewise. This increased activity usually became noticeable by the time the temperature in the experiment had been raised as little as 2° C. above that of the control. With the gradual rise in the temperature of the experimental pan, the activities of the experimental fish became more and more marked until in a number of instances the fish attempted to leap out of the pan at a temperature still 2°-3° C. below the maximum for the species. At this point the swimming movements were still in perfect correlation, but, as the temperature approached the maximum for the species, lack of correlation began to develop and at a temperature of 1° C. or less, below the maximum, a sudden paroxysm set in. The fish "scooted" blindly about the pan, sometimes shooting over the edge. This intense activity lasted for about 30 seconds or less, when the fish fell to its side, making no visible movements other than feeble twitchings of the gills and fins. If at this point it was immediately removed and placed in cooler water it often recovered; the possibility of recovery varied with the species and size of the fish, the more hardy species (bull-head) and the larger individuals of the other species (cyprinids) being most likely to live. The paroxysm induced by temperature resembled so much that produced in other experiments (Wells '13) by lack of oxygen and excess carbon dioxide, that analyses were made to determine the amount of these gases present during the experiments. These analyses always showed a normal amount of oxygen to be present while the amount of carbon dioxide was if anything a little less than that of the control, the diminution being due to the higher temperature of the experiment.

In the attempt to determine a definite maximum temperature for the different species used it was found that a number of factors must be considered. The species used all resisted higher temperatures when the heating was gradual, than they did when it was comparatively rapid, thus showing some acclimatization to the higher temperatures. Large fishes of a given species were usually considered more resistant than were small ones of the same species. The physiological condition of the species was found to be important; it has been found that practically all the species of fishes occurring in the rivers and creeks in the vicinity of Chicago are a great deal more resistant to many kinds of stimuli, temperature included, in March and April, just before the breeding season begins, than they are in the latter part of June and first part of July, immediately following the breeding season. In fact resistance is so low at this latter time of year, that most of the species of cyprinid minnows cannot be transported into the laboratory from creeks an hour's ride out, even though ice be taken along to keep the water cool. So low is the resistance at this time that these species often die from the shock of being seined out of the water and transferred to the fish bucket. Thus, if one were to draw the seasonal resistance curve of such fishes, it would be a rather regular curve, the highest point occurring in March and April and the lowest point in the latter part of June and first part of July, with the difference in the level of these two points a considerable one. From the low point the rise in resistance is very slow and gradual up to the latter part of September when the curve begins to rise more rapidly up to the high point in the spring.

For the above reasons it has been found impossible to state that any certain temperature is the maximum which can be endured by a given species. There are, however, definite specific differences in the resistance of fishes to temperature as well as to other factors. Of the species used in the experiments, the black bull-head (*Ameiurus melas*) was the most hardy, even though none but young of this species was used. This species could be raised to 35°-36° C. before death occurred. The other species follow in the order of their increasing resistance. Silver shiner (*Notropis atherinoides*) 27°-28° C.; straw-colored minnow (*Notropis blennius*), 28°-29° C.; common shiner (*Notropis cornutus*), 28°-30° C. (Temperatures are approximate). Field and experimental observations have been made upon a large number of other species, but will not be tabulated here.

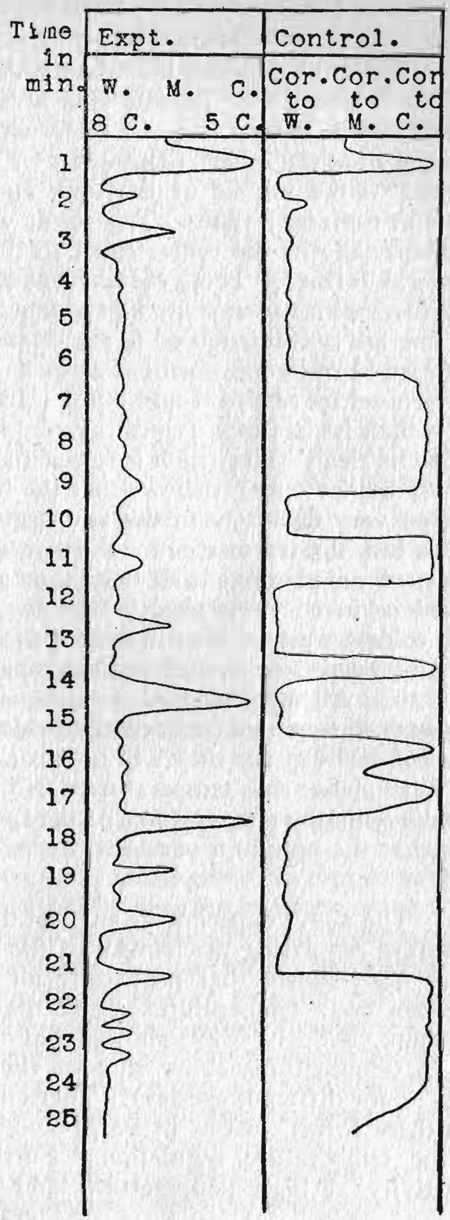
In experiments where fishes were subjected to sudden changes of temperature, the changes were made through a large number of the possible combinations existing in a range of temperature, the highest point of which is just below the general maximum for the species and the lowest point, one or two degrees above freezing. Thus one series of experiments consisted in changing adults of *Notropis blennius* from 28° C. to 3° C., from 25° C to 3° C.,from 22° C. to 3° C., and so on down to a last change of from 10° C. to 3° C. In all the experiments the method employed was to arrange the pans of cold and warm water along side each other. The temperatures of these pans were kept constant for each test. The fish was quickly lifted from one pan to the other in the direction in which the change was to be made, i. e., from warm to cold or vice versa. The general effect of change from colder to warmer is, as has been noted, to increase the activity of the fish; the reverse change tends to diminish these activities. In general this increase or decrease of activity proceeds regularly and proportionately with the change in temperature, but at the higher and lower limits of temperature used in these experiments, there is a breaking over the bounds of normal activity and a period of abnormal activity ensues. This period has been described in the case of high temperatures, where it comes on as the temperature nears the death point for the species, and it will occur whether the heating be slow or rapid, the only difference being that with slow heating, it occurs at a higher temperature than when the heating is rapid (.5°-1.5° C. difference for the different rates tried). In the experiments where the fishes were changed from warmer to colder water it was found that with certain changes a paroxysm of activity similar to that of heating follows the transfer. To produce this result the temperature change must be sudden and relatively great. With *Notropis blennius* adults, for instance, a sudden change into water which is at least 10° C. colder than that in which the fish has been kept will produce upon the part of the fish violent activities, providing the lower temperature is not above 5°-6° C. Thus a sudden change from 15° C. to 3° C. will give the reaction, while a change from 25° C. to 13° C. will merely result in a decrease of normal movements, as rate of gill contractions, etc. A gradual cooling of the surrounding water does not result in any marked reaction at any point down to freezing (Heath '83). A typical experiment will illustrate this reaction in which the paroxysm, due to change from warmer to colder temperature occurs. "An adult *Notropis blennius* was suddenly transferred from water whose temperature was 13° C. to water of 3° C. The fish had been kept in the 13° water for four days. When dropped into the cold water, it lost all motion and gill movements could scarcely be detected. It lay thus on its side for 1 minute and 30 seconds; began to swim a little, and then suddenly "scooted" madly about the pan. This blindly violent activity lasted for 5 seconds; fish again fell to side; lay motionless for 5 seconds; pectoral fins began to twitch; gill movements weak and irregular; gradually movements of gills and fins became more vigorous until at end of 22 minutes, fish was swimming about pan; still unable to maintain equilibrium; at end of 34 minutes floating easily and normally in the cold water." The bull-head does not show any such marked reaction, however great the temperature change, its adjustment remaining within the bounds of normality in all changes from warmer to colder water. Small cyprinid fishes were less affected by the change from warm to cold than were adults of the same species, the small fishes as a usual thing not passing through a paroxysm in adjusting to the lower temperature; in any case the time required to regain normality was always less in the case of the smaller (younger) fishes of a given species. It will be remembered that the reverse was the case with regard to resistance to high temperatures. In no case was death the result of sudden change from higher to lower temperatures, though the widest range possible between the specific maximum and freezing was tried. It may well be, however, that sudden lowering in temperature does result in death where certain species are concerned. In the planting of trout fry in cold mountain streams, the change from the warm water of shipping cans into the cold water of the stream has been blamed for the high percentage of death on the part of the fry in some cases. It is a common custom among fish culturists to cool the water in the cans gradually down to the temperature of the stream, by gradually adding the colder water to that in the cans. Sudden changes from lower to higher temperatures often result in marked temporary increase in activity, but there is no loss of correlation of movements unless the higher temperature is near the maximum for the species.

In another series of experiments it was found that the time which is required for a fish to become normal in cold water is proportional to the time which it has been in the water of higher temperature. This proportionality does not hold after the fish has been in the warm water for more than an hour or two, as the fish seems to become completely adjusted by that time and further stay does not alter its actions when returned to cold water. In one series of experiments of this sort, it was found that if an adult *Notropis blennius* is transferred from 3° C. to 15° C. water for 1 minute and then back into the 3° water, it is noticeably affected, but is normal within 1 minute. If left in the warm water 5 minutes, is normal in 5 minutes after being returned to the cold; 10 minutes in warm, normal in 7 minutes in cold; 20 minutes in warm, normal in 10 minutes; 40 minutes in warm, normal in 15 minutes in cold. Up to this point adults of this species always became normal in the cold water without passing through the paroxysm. When left in the warm water for 50-60 minutes, however, the paroxysm occurred 1 minute after transfer to the cold. Further stay in the warm water had no increased effect except to increase somewhat the total time elapsing before complete equilibrium in the cold water was established. A single fish could be made to pass through the paroxysm many times, the only permanent adjustment upon the part of the fish being a slight increase in its ability to resist the shock of the sudden change from warm to cold. This was indicated by the fact that to produce successive recurrences of the paroxysm, the temperature change had to be made successively larger or the fish left for a successively longer time in the warmer water.

2. *Reaction of Fishes to Temperature*: Under this head are included a number of experiments which were performed by putting the fishes into a long narrow tank arranged so that the water flowing in at one end was of a different temperature from that flowing in at the other. The water of the two temperatures flowed to the middle of the tank and thence out through drains at top and bottom. The result was a mixing of the water, especially of the center third so that a temperature gradient was formed. This gradient was accurately determined by testing with thermometers graduated to tenths of a degree C. The fish was introduced at the center of the tank and a graph (Fig. 1) of its movements was made according to the method first used by Shelford and Allee ('13). A glance at the figure, which is that of a typical graph, will make the method and results clear. The graph is selected as typical of a large number of similar ones; it shows that the fish in the experiment reacted very definitely to the temperature gradient, selecting in this case the warmer end. Furthermore it will be noted that most of the turnings back from the colder portions of the gradient occurred some time before the fish had encountered the coldest water. Measurements showed that the fish detected and reacted to variations in temperature of no more than .1° C. All species tried were equally sensitive. Other experiments showed that fishes tend to select an optimum temperature (16°-19° C.) for they will turn back from warm water when it is above this temperature. No attempt was made to alter the optimum temperatures of the species used but it is probable that the optimum varies with the physiological state.

Discussion: The above experiments suggest that fishes possess a temperature regulating mechanism of the most delicate order. It has been shown that practically all cold blooded animals maintain body temperatures above that of the surrounding medium. Kidder (1879) showed that certain marine fishes maintain temperatures above that of the surrounding water (5°-20° C for different species). There must therefore be present in these forms, just as in warm blooded animals, a mechanism for temperature regulation. Furthermore, the convulsive activity at high temperatures and upon sudden

Figure 1, showing the reaction of a small (4 in.) micropterus dolomieu to a temperature gradient. The graph in the experiment shows a decisive selection of the warmer end. The control is neutral. Headings in control mean "Corresponding to Warm." etc.



changes to lower temperatures may be due to a failure of the mechanism to adjust to the extreme change. This explanation is supported by the fact that more adjustment was made in the case of slow heating than in the case where heating was rapid, and also by the fact that complete adjustment took place when cooling was slow. Thus acclimatization to temperature may be looked upon as resulting from an adjustment of the temperature regulating mechanism.

Experiments upon the rate of metabolism under different temperature conditions have not been carried out as yet. Just how the rate of reaction is affected, for instance, by raising the temperature of the water surrounding a fish is not certain. It is probably correct to state that in general the rate of metabolism is increased with increase in temperature, and diminished with decrease. But whether or not each degree's rise or fall in temperature increases the carbon dioxide output to the same extent is a question. Very probably the effect upon the metabolism, of changes in temperature is not the same at different points in the temperature scale, that is to say, the metabolism of a fish at 3° C. may differ from its metabolism at 25°C., not only quantitatively but qualitatively as well. Furthermore the factors that cause the fish to pass into a state of uncontrolled convulsive activity at the stages of heat and cold rigor and what heat and cold rigor are in themselves, are questions that can be answered only by means of quantitative experiments which are yet to be undertaken. At this time it seems plausible to look upon these reactions as outward manifestations of qualitative or cumulative quantitative changes in the metabolism of the organism.

TEMPERATURE AND THE DISTRIBUTION OF FISHES

It is interesting to find that forms where the activities of the individuals are so dependent upon the conditions of the surrounding environment, possess exceedingly delicate mechanisms for the detection of environmental changes. Thus it has been shown that they are able to recognize very minute differences in acidity, (Shelford and Allee, '13), (Shelford, '14) and in the foregoing pages we have seen that they are also exceedingly sensitive to slight changes in temperature, their sensitiveness in this respect far exceeding that of warm blooded animals. This fact becomes a suggestive one when thought of in connection with the life activities of fishes and the resulting distribution of these forms through their reactions. (The relation of resistance to reaction has been discussed in a former paper (Wells, '13) and will not be taken up here. If fishes can detect and will react to so small a variation in the temperature of the surrounding water as 1° C., it must be that they are continually reacting to this factor in all fish environments for such small differences in temperature must exist even in the smallest body of water. It has been suggested that temperature has much to do with the migrations of salt water fishes into fresh water streams, and the reaction experiments here outlined furnish support for such an idea. We must not attempt to limit the accuracy of such migrations to the temperature factor, however, for there are many other factors to be considered. Undoubtedly density, salinity, gaseous content, and acidity, as well as temperature, play their part in this phenomenon. The final solution of the problem must take all factors into consideration.

Summary: 1. The resistance of fishes to temperature varies with the species and with the size of the fish. Large fish of a given species are more resistant to high temperatures than small fish of the same species, but the small fish adjust to sudden changes from warm to cold more successfully.

2. There is no definite maximum temperature for a given species of fishes; the maximum varies with the rate of heating, with the size of the fish and with its physiological condition.

3. Fishes detect and react to exceedingly small (.1° C.) variations, in the temperature of the surrounding water.

4. Both the resistance and the reaction experiments indicate that the fishes experimented upon, possess a temperature regulating mechanism which is much more delicate than that of the warmer animals, though not as efficient in maintaining a constant body temperature.

5. The effect of temperature upon the migrations and distribution of fishes is obvious, since variations in temperature, far in excess of the minimum variation to which fish will react, are known to occur constantly in fish environments.

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