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THE QUARTERLY REVIEW of BIOLOGY



SOME PRINCIPLES IN THE THERMAL REQUIREMENTS OF FISHES

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INTRODUCTION

THE tissues of a fish, permeated by the network of the circulatory system, are constantly being brought into equilibrium with the external temperature at the gill surface. The high specific heat of water, which efficiently buffers the aquatic climate from the extremes of aerial conditions, has chained the gill-respiring vertebrate to a cold-blooded existence. To achieve regulation of body temperature requires control of the temperature at the respiratory surface or of the circulatory fluid, as well as of the body tissues. Insulation of the gills by means of fat deposition would defeat their primary purpose for oxygen uptake. Alternatively, the energy exchange required to bring the volume of water necessary for adequate respiration up, or down, to a satisfactory body temperature would frequently be exhausting. Evaporation, the chief physical aid for heat loss in an air-breathing vertebrate, is denied the gill-respiring vertebrate; adaptations to an aquatic life leave it entirely subject to the variations of environmental temperature. Measurements of the body temperature of fish and other aquatic poikilotherms confirm this relation, the equilibrium state being reached more rapidly among small than large forms (S. Simpson, 1908; Pearse and Hall, 1928; Nielson, 1938; Gunn, 1942; Davis, 1955).

Minor exceptions may arise through heat pro-

duction from excessive activity, particularly for a fish caught by some means which prevents normal respiration, or through the rapid excursion from one level of thermal stratification to another (Morrow and Mauro, 1950). At near-lethal, low temperatures the effect of greatly reduced respiration may permit body temperatures to be temporarily maintained above that of the environment. Measurements of the stomach temperature of brown bullheads (*Ameiurus nebulosus*) when taken from 20°C. and placed in ice-water showed an internal temperature of 0.3° to 0.5°C. above the external temperature after two hours of immersion. (Previously unreported observations made at the Ont. Fish. Res. Lab., Algonquin Park, Ont.)

Lacking a means of maintaining an independent body temperature, the aquatic poikilotherm may be a victim of rapid internal temperature change caused by sudden changes in environmental temperature. The response of many fish when plunged into relatively cold water is one of violent bursts of activity followed by benumbed inactivity. Such a temperature change, although acting as a strong stimulus, simultaneously depresses the animal into temporary dormancy. The conflict of combined stimulation and depression is quite striking. Because of the all-pervading nature of environmental temperature, the fundamental thermal requirement of fishes is an *external* environmental temperature most suitable to their

internal tissues. That this temperature may not be limited to a matter of a few degrees attests the extent to which the poikilotherm has been able to evolve bodily functions which can maintain adequate roles *despite* variation in body temperature (cf. Bullock, 1955).

Temperature sets lethal limits to life; it conditions the animal through acclimation to meet levels of temperature that would otherwise be intolerable; it governs the rate of development; it sets the limits of metabolic rate within which the animal is free to perform; and it acts as a directive factor resulting in the congregation of fish within given thermal ranges, or movements to new environmental conditions. Some of the principles in this multiple role of temperature will be considered.

LETHAL LIMITS

Upper and lower lethal temperatures

The upper and lower limits of temperature which fish can withstand define the extremes of tolerable thermal environment. While a variety of experimental procedures have been used to determine the lethal limits (Loeb and Wasteneys, 1912; Hathaway, 1927; Fry, Brett, and Clawson, 1942; Doudoroff, 1942), in each case an effort has been made to provide a simple index, usually expressed as the mean or median temperature tolerance for an unselected sample of fish when exposed for some predetermined interval of time. A number of distinct characteristics of the lethal temperature have been repeatedly demonstrated. Under carefully controlled conditions the upper lethal temperature is remarkably precise. It can be determined consistently in many species to within $\pm 0.2^\circ\text{C}$. This sensitivity has permitted a comparison of species tolerance, with significant differences obtained between closely related species (Brett, 1952) and some subspecies (Hart, 1952). Indeed, Gibson (1953) has obtained data which suggest that temperature resistance in the guppy (*Lebistes reticulatus*) can be affected by selective breeding. In addition, species which show similar upper lethal limits may be characterized by quite different lower levels of tolerance. The order of temperature resistance (heat-tolerance) among eight species of freshwater fish from Algonquin Park lakes, Ontario, was reversed for half these species when they were tested for cold-tolerance (Brett, 1944).

The lethal limits are only consistent within a species when repeated for fish from similar acclimation temperatures and cultured under comparable conditions (cf. Hoar and Cottle, 1952a; Gibson, 1953). As the temperature of acclimation increases, so the lethal temperatures progressively increase. For the goldfish (*Carassius auratus*) Fry et al. (1942) report that for every 3°C . rise in acclimation temperature the rate of change of the upper lethal temperature was about 1°C ., and that for the lower lethal temperature nearly 2°C . A considerably lesser rate of change was obtained for yearling speckled trout (*Salvelinus fontinalis*), which required a 7°C . change in acclimation to produce a 1°C . change in the upper lethal temperature (Fry, Hart, and Walker, 1946). The rate of increase is not constant throughout the full range of acclimation, but usually "levels off" to zero in the region of relatively high acclimation for each species. The fact that the lethal temperatures are subject to change through acclimation has led to the calculation of the area enclosed within upper and lower lethal ranges, for temperatures of acclimation from 0°C . to the maximum for any given species (Fig. 1; Table 1). This defines the *zone of tolerance*, with the unit of tolerance equal to the area bounded by 1°C . (expressed as "degrees Centigrade squared"). The extent of eurythermicity of the organism

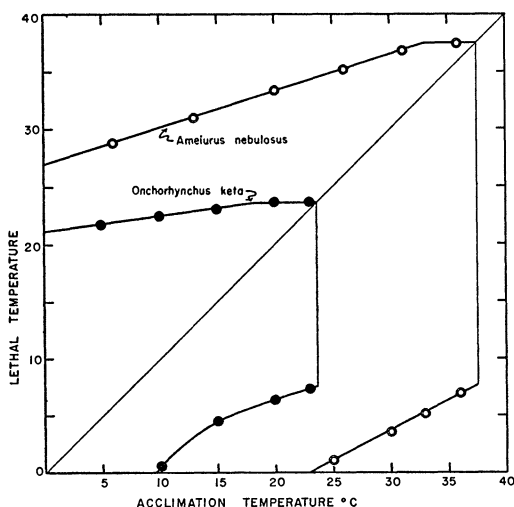


FIG. 1. LETHAL TEMPERATURE RELATIONS FOR TWO SPECIES OF FISH

The bullhead, *Ameiurus nebulosus*, is a highly tolerant species in contrast to the chum salmon, *Oncorhynchus keta*, which is one of the least resistant studied to date. The area enclosed by each trapezium is the *zone of tolerance*. (Data from Brett, 1944 and 1952).

TABLE 1

Lethal temperatures and thermal tolerances of various species of fish arranged in order of thermal tolerance

Species	Family		Upper (U.) and Lower (L.) lethal temperatures for acclimation temperatures of:						Thermal tolerance	Habitat	Reference
			5°C.	10°C	15°C	20°C	25°C.	30°C			
<i>Oncorhynchus gorbusha</i> *	Salmonidae	U.	21.3	22.5	23.1	23.9			450†	Cool streams	7
		L.									
<i>Oncorhynchus keta</i> *	Salminidae	U.	21.8	22.6	23.1	23.7			468	Cool streams	7
		L.		0.5	4.7	6.5					
<i>Oncorhynchus nerka</i> *	Salmonidae	U.	22.2	23.4	24.4	24.8			505	Cool streams, deep lakes	7
		L.	0.0	3.1	4.1	4.7					
<i>Oncorhynchus kisutch</i> *	Salmonidae	U.	22.9	23.7	24.3	25.0			528	Cool to moderately warm streams and lakes	7
		L.	0.2	1.7	3.5	4.5					
<i>Oncorhynchus tshawytscha</i> *	Salmonidae	U.	21.5	24.3	25.0	25.1			529	Cool streams	7
		L.		0.8	2.5	4.5					
<i>Salvelinus fontinalis</i>	Salmonidae	U.	23.7†	24.4†	25.0	25.3	25.3		625	Cool streams, deep lakes	4
		L.					0.5				
<i>Perca flavescens</i>	Percidae	U.	21.3	25.0	27.7		29.7		742	Deep and shallow lakes	5
		L.		1.1			3.7				
<i>Notropis atherinoides</i>	Cyprinidae	U.	23.2	26.7	28.9	30.7	30.7		747	Shallow lakes, cool streams	5
		L.			1.6	5.2	8.0				
<i>Catostomus commersonni</i>	Catostomidae	U.	26.3	27.7	29.3	29.3	29.3		770	Shallow lakes, warm and cool streams	5
		L.				2.5	6.0				
<i>Rhinichthys atratulus</i>	Cyprinidae	U.	26.5	28.8	29.6	29.3			790	Warm and cool streams	6
		L.				2.2					
<i>Girella nigricans</i>	Stromateidae	U.		28.7		31.4		31.4	800	Shallow marine bays and pools	2
		L.		5.0		8.0		13.0			
<i>Notropis cornutus</i>	Cyprinidae	U.	26.7	28.6	30.3		31.0	31.0	803	Shallow northern lakes. Cool and warm streams	5
		L.			0.0	3.7	7.8				
<i>Semotilus atromaculatus</i>	Cyprinidae	U.	24.7	27.3	29.3	30.3	30.3		808	Lake shallows, warm and cool streams	6
		L.				0.7	4.5				
<i>Dorosoma cepedianum</i>	Clupeidae	U.					34.3	35.9	880†	Shallow, open water	6
		L.					10.8	14.5			
<i>Hyborkhynchus notatus</i>	Cyprinidae	U.	26.0	28.3	30.6	31.7	33.3		884	Shallow lakes, slow streams	5
		L.			1.0	4.2	7.5				
<i>Pimephales promelas</i>	Cyprinidae	U.		28.2		31.7		33.2	903	Shallow lakes	5
		L.				1.5		10.5			
<i>Lepomis macrochirus</i>	Centrarchidae	U.			30.7	31.5		33.8?	910†	Shallow lakes	6
		L.			2.5	5.0	7.5	11.1?			
<i>Notemigonus crysoleucas</i>	Cyprinidae	U.		29.3	30.5	31.8	33.2	34.7	940	Warm and slow, cool streams	6
		L.			1.5	4.0	7.0	11.2			
<i>Micropterus salmoides</i>	Centrarchidae	U.				32.5	34.5	36.4	965†	Marsh and shallow reed beds	6
		L.				5.5		11.8			
<i>Ictalurus lacustris</i>	Ameiuridae	U.			30.3	32.8	33.5		970†	Large rivers and warm lakes	6
		L.			0.0	2.5	6.0				
<i>Gambusia affinis</i>	Poeciliidae	U.			35.4	37.3	37.3	37.3	1110†	Marsh, very shallow reed beds	6
		L.			1.5	5.5					
<i>Ameiurus nebulosus</i>	Ameiuridae	U.	28.6	30.2	31.8	33.4	35.0	36.5	1162	Marsh; shallow zone of lakes	3
		L.				-1.0	1.3	3.7			
<i>Carassius auratus</i>	Cyprinidae	U.	29.0†	30.8	32.8†	34.8†	36.6†	38.6†	1220	Very shallow water	1
		L.				2.0	6.0	9.0			

* Freshwater fry stage only.

† Estimate from graph by interpolation.

‡ Provisionary, pending more data.

References: (1) Fry, Brett, and Clawson, 1942; (2) Doudoroff, 1942; (3) Brett, 1944; (4) Fry, Hart, and Walker, 1946; (5) Hart, 1947; (6) Hart, 1952; (7) Brett, 1952.

can thus be readily determined. Hart (1947) ascertained the lethal effects of temperature for eight species of fish from the Toronto region and made comparisons with results reported elsewhere in the literature. Since then Hart (1952) has published further studies on lethal temperatures; and results on temperature tolerance in young Pacific salmon have been reported by Brett (1952). These data are summarized in Table 1. Some generalities can be derived.

The Salmonidae have the lowest thermal tolerance found to date, with maximum upper lethal temperatures barely exceeding 25°C. The sea-migratory forms (*Oncorhynchus*) have considerably less resistance to low temperatures than is indicated for the lake and stream-dwelling char (*Salvelinus fontinalis*); indeed the latter has a greater cold-tolerance than any species yet reported.

With the exception of the goldfish (*Carassius*), the Cyprinidae occupy a somewhat intermediate position, with thermal tolerances ranging from levels approaching but distinctly above the Salmonidae, the difference resulting more from a resistance to high than to low temperatures. Through acclimation, an upper lethal temperature exceeding 30°C. is achieved by most members of this family.

The thermal tolerances of the single members studied from the families Percidae, Stromateidae, and Catostomidae occur at the low end of the range for the cyprinids, whereas the two centrarchids are towards the upper end.

The Ameiuridae appear to occupy the top position among the most eurythermal, along with the goldfish. The common bullhead (*Ameiurus nebulosus*) is also particularly resistant to low temperatures.

Black (1953) has made a comparison of upper lethal temperatures for similar and closely related species studied in British Columbia with those from Ontario (Brett, 1944; Fry et al., 1946; Hart, 1947) and some parts of the United States (Hart, 1952). Although variations can be seen to exist, these cannot be entirely ascribed to different geographic locations, owing to slight differences in experimental technique and the question of exact acclimation temperatures. However, the general conclusions are essentially the same as established elsewhere. One recurring exception appears to exist in the case of the largemouth bass (*Micropterus salmoides*); which Hart (1952) also reported

to show significant geographic differences. It would be of interest to culture eggs taken from these separate populations under identical conditions and to establish unequivocally the degree of inherent physiological difference.

Resistance times

The lethal temperature is theoretically conceived as that temperature which fifty per cent of a population could withstand for infinite time. Experimentally it is obtained by subjecting samples of fish to a series of temperatures, higher levels of which result in complete mortality of the sample. The period of tolerance prior to death is known as the *resistance time* (Fry, 1947a). By plotting the logarithm of the median resistance time (i.e., the resistance of the most representative fish) for each of a number of test temperatures, the points are seen to form a linear series, the slope of which is relatively consistent for most species of fish, despite very different levels of resistance (Fig. 2). In each case an abrupt change in slope occurs, marking the point of transition from *resistance* to *tolerance* and signifying that death from temperature as a primary cause has ceased. This temperature is the *incipient lethal temperature*.

By virtue of this resistance it is possible for fish to make excursions for limited times into temperature zones which would eventually be lethal.

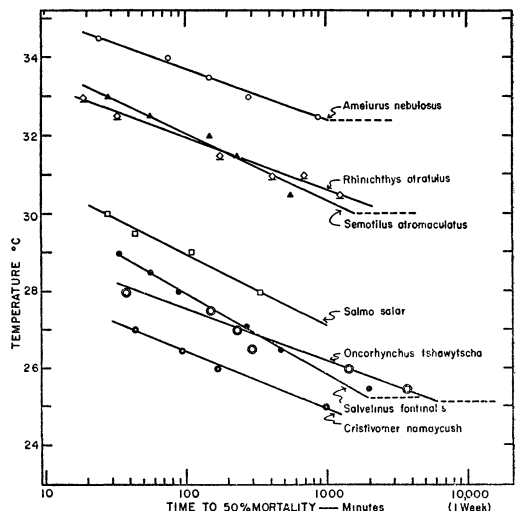


FIG. 2. MEDIAN RESISTANCE TIMES FOR SEVEN SPECIES OF FISH ACCLIMATED TO 20°C. Broken lines indicate incipient lethal level. (Data from Fry, 1947b; Hart, 1952; Brett, 1952).

It also permits them to tolerate some diurnal fluctuations in which the peaks of environmental temperature actually exceed the lethal temperature (Fry et al., 1946).

Possible cause of death

The life of an animal can be maintained only in conjunction with the continuous functioning and integration of the majority of its tissues. The thermal lethal level must be set by the resistance of the most sensitive essential tissue. This tissue, for upper lethal temperatures, appears to be that of the nervous system. Freeman (1950) discovered that the metabolic activity of goldfish brain tissue approached zero at a temperature approximating the ultimate upper lethal temperature reported for this species by Fry et al. (1942). A pronounced depression, though not a cessation, in the rate of oxygen uptake of excised brain tissue from the largemouth black bass is reported to occur at 35°C. (Fuhrman, Hollinger, Crimson, Field, and Weymouth, 1944). The bass had been collected in a reservoir with surface temperatures ranging to 24°C. It is of interest that Hart (1952) obtained an upper lethal temperature of 34.5°C. for this species when acclimated to 25°C. In some fish the cause of death from high temperatures may possibly result from the inactivation of the respiratory center, followed by death from oxygen lack. The respiratory movements of the yellow perch (*Perca flavescens*) cease entirely with the approach of heat-death (Brett, 1944). Battle (1926) subjected muscle and nerve tissue of the skate (*Raja radiata* and *R. erinacea*) to gradual heating. Inactivation of the nerve tissues preceded that of the somatic and smooth muscles.

Death from intolerably low temperatures has also been attributed in some instances to failure of the nervous system. However, it is now known that thermal death may not always arise from the same cause. Doudoroff (1942) distinguished stages of "primary" and "secondary chill-coma" among samples of *Girella nigricans* when subjected to low temperatures. "Primary chill-coma" was not manifest until some seconds after immersion and apparently did not stimulate the cutaneous sense organs but penetrated to the central nervous system. A similar phenomenon was observed among young Pacific salmon (Brett, 1952). Experiments performed in saline solutions, slightly hypertonic to blood concentrations, indicated that three causes of death from low temperature

were involved: one, a very rapid agent, usually effective within 60 minutes of exposure and probably a disturbance of the central nervous system; a second, which was related to osmotic balance; and a third, delayed in time of onset, and of unknown origin.

Peiss and Field (1950) studied the oxygen consumption of excised brain and liver tissues from the cold-adapted polar cod (*Boreogadus saida*) and compared these with similar studies on the warm-adapted golden orfe (*Idus melanotus*). The polar cod, obtained from waters ranging from -1.5°C. to +2.0°C., showed an ability to maintain a consistent rate of oxygen uptake of its tissues at all temperatures from 0°C. to 25°C. That of the orfe, although fairly similar for higher temperatures, was considerably reduced at levels below 10°C. In contrast, the period of sustained tissue respiration was progressively curtailed above 15°C. in the cod, whereas the orfe was capable of maintaining its uptake at all temperatures studied. In both cases the oxygen demand of brain tissue was greater than that of liver tissue. The authors concluded that the tissues of the polar cod were advantageously adapted to cold. Adjustment in the metabolic demand of the total organism to the appropriate climatic conditions has been studied by Scholander, Flagg, Walters, and Irving (1953). A comparison between some arctic and tropical fishes indicated that the cold-adapted forms were likewise capable of a higher rate of oxygen uptake at comparable low temperatures. When actively swimming, the arctic fishes expended a greater proportion of their available energy per unit time than did the tropical forms. That is, the routine act of locomotion is maintained much nearer the maximum level possible among arctic than tropical fishes at their respective normal environmental temperatures.

Hoar, in conjunction with Dorchester (1949) and later Cottle (1952a, b), has examined the effect of dietary fats of different melting points on the temperature tolerance of gold-fish, and made an effort to ascertain the nature of the thermal death of tissues. Although significant changes in resistance to high and to low temperatures were demonstrated, no direct relation between tolerance and the melting point of ingested fats was obtained. These authors believe that the integrity of the plasma membrane and its permeability is associated with the presence of unsaturated lipids in the structure of the membrane.

If the limiting tissue responsible for death from extremes of temperature is that of the nervous system, a critical examination of changes in this tissue separately is warranted.

Rate of acclimation

The varying ability among fishes to extend their temperature tolerance through acclimation has been illustrated. While the principle of acclimation, or more generally acclimatization (used synonymously with acclimation, cf. Bullock, 1955), has been recognized since the last century (Davenport and Castle, 1895), surprisingly little study has been devoted to this phenomenon. It would appear that the rate of increase in ability to tolerate higher temperatures among fish is relatively rapid, requiring less than 24 hours at temperatures above 20°C. (Doudoroff, 1942; Brett, 1944). Conversely, the loss in this increased tolerance, and the gain in resistance to low temperatures, are inherently slower processes, requiring up to 20 days in some species to approach completion. These rates appear to be governed by the rate of metabolism, which, if depressed by a low environmental temperature, automatically reduces the rate of acclimation. Whatever the process, Brett (1944) discovered that acclimation to a higher temperature in the bullhead was inhibited under conditions of low oxygen concentration.

It must therefore be a characteristic of at least the most sensitive tissue, or the integrating system (e.g., myoneural junction, nerve synapse), to be capable of rapid and reversible changes in temperature tolerance. Such a fish as the bullhead can increase its heat-tolerance by 10°C., whereas the speckled trout is limited to less than 5°C. Although fish lack a thermal control mechanism, their capability of inhabiting a wide range of thermal environments has been achieved by the development of remarkably tolerant tissues, and has been extended through acclimation. It is possible to culture goldfish over a range of 40°C. The homoiotherm has sacrificed this tissue tolerance, supplanted as it is by the considerably increased limits of tolerance to extremes of environmental temperature which thermal control has provided for the intact organism.

Ecological significance

There can be no doubt that the lethal temperature exerts limiting effects on the geographic

distribution and freedom for successful existence in the confines of lake and stream, or the strata of the ocean. Fry (1951) has assembled much of the existing evidence for the environmental relations of temperature in the speckled trout (cf. Creaser, 1930; Ricker, 1934). The agreement between field and laboratory findings is convincing. Crises, when temperatures reach 24°C. to 27°C., can be survived only for short periods (Huntsman, 1946). However, the ability of fish to survive near-freezing temperatures is annually demonstrated in ice-covered lakes.

Somewhat in contrast to these are the temperature relations for six species of freshwater fish from lakes in Algonquin Park, Ontario (Brett, 1944). Seasonal changes in the upper lethal temperatures were determined for samples of fish from locations in which recording thermometers had been placed. In every instance the lethal temperatures rose rapidly with ascending lake temperatures, exceeding the daily lake maxima by 6° to 8°C. The highest seasonal lethal temperatures recorded for the six species ranged from 32°C. to 35°C., yet the full scope for temperature tolerance had not been tapped, as laboratory experiments revealed. The ability to exceed considerably the highest environmental temperatures to be expected in the common range of the species signifies that lethal relations must play a relatively unimportant role in the limiting of many hardy species, at least in the post-embryonic stage. Yet, in their general order of increasing heat-tolerance, they show a correlation with an ecological succession from cold streams and deep lakes to warmer streams and littoral zones, and finally to marsh conditions (Hart, 1952; Table 1, this paper). Some other property or attribute of the organism, roughly reflected by the upper lethal temperature, must be operating as the restricting factor to distribution.

Few cases of heat-death among fish are recorded in the literature (Bailey, 1955). Cold-death, however, has been reported more frequently (Verrill, 1901; Storey, 1937; Gunther, 1941; Galloway, 1941). Although the threat to existence appears to come more from conditions of low temperature than of high temperature, the correlation between lower lethal temperatures and habitat is even less apparent than for upper lethal temperatures. This may be attributed in part to a characteristically slow rate of gain of cold-tolerance among fishes. It is the *rapidity* of the onset of low temperatures

that probably causes death, outstripping the ability of the fish to acclimate to a lower level, despite being within its biokinetic range.

Severe cold in the North Sea, as reported by A. C. Simpson (1953), appears to have exceeded the lower lethal temperatures for plaice, cod, whiting, and dab despite the probability that time did permit maximum acclimation. Nevertheless the author relates that "continuous cold easterly gales caused rapid cooling of the surface water." The lowest surface temperature recorded was -1.8°C . and a probable minimum bottom temperature of 0°C . (Vaux, 1953). The freezing point of the body fluids of teleosts lies mainly within a range of -0.5°C . to -0.9°C . (Dakin, 1912; Krogh, 1939; Kubo, 1953).

The state of thermal acclimation of the bullhead was traced by Brett (1944; 1946) from May to September in Lake Opeongo. The ability of this species to achieve a high level of acclimation as the environmental temperature rose rapidly in spring provided adequate safeguard for the high temperatures in the shallow reed beds of its habitat. As a result of the rapid acclimation to high temperatures, coupled with a slow loss of this recently acquired tolerance, acclimation kept pace with the daily lake water maxima.

The inability among young salmon to cope with osmotic stress at low temperatures would suggest that the estuarian conditions of moderate salinity would provide some sanctuary from cold-death.

DEVELOPMENTAL STAGES

As has been suggested, extremes of temperature can be withstood by many fishes to a degree which considerably exceeds the normal peaks of their environmental temperature; and habitat correlations with lethal temperatures are but grossly apparent. This applies only to the free-swimming, fully-formed fish. Precise knowledge of thermal tolerance and, more generally, the thermal requirements for the egg, developing embryo, and larval stages is scant (cf. Bonnet, 1939). There are inherent difficulties in determining the effects of temperature on an organism during a period of such rapid cellular change, particularly in the light of the importance of acclimation.

For animals in general, Baldwin (1948) comments that "at certain periods, notably at the time of gastrulation, the developing embryo is particularly susceptible to thermal and other changes." Battle (1929) discovered that the early

blastodermic stages of the rockling (*Enchelyopus cimbrius*) were most susceptible to heat death. Abnormalities were produced by lowering the temperature of the ova to 5°C . Embury (1934) and Hayes (1949) have conducted research and reviewed much of the available information concerning the effects of temperature on salmonoid eggs. Interest has been centered on the incubation period and growth relations within a viable range of temperatures, embracing extremes of 1.5°C . (speckled trout) and 17.6°C . (rainbow trout). There is nothing to indicate that normal development is not possible throughout this span. The growth relation, however, shows some inconsistencies at the extremes. The theoretical relation of " $\text{temperature } (^{\circ}\text{C}) \times \text{time} = \text{constant}$ " applies quite well from 4 to 14°C . Deviation at lower temperatures would suggest that hatching is possible at 0°C . Embury, referring to the work of Dannevig (1894), notes that eggs of a marine fish, the cod, "were partly or wholly developed in sea water over a temperature range from -1 to $+14^{\circ}\text{C}$."

Salmon and trout hatcheries are usually located near a natural source of cold, clear, running water. The necessity for low temperatures in artificial propagation, however, arises as much from avoiding disease under the unnaturally crowded conditions, as from obtaining a suitable temperature for development and hatching. Undoubtedly the migrations to cool, freshwater streams are necessary for the survival of the salmon species, from a thermal as well as an osmotic requirement. The embryonic stage of many coldwater fishes is passed during the winter and early spring, the fry emerging as the temperatures begin to rise. Relatively uniform low temperatures prevail. Pacific salmon (*Oncorhynchus*) eggs have been found to be viable under thin sheets of ice, locking the surface gravel like cement. When death occurs it has frequently been attributed to desiccation, oxygen lack, or disease rather than low temperature, although such a diagnosis is usually speculative.

It can be stated at least that the thermal requirements in the very early stages are more exacting than in the adult.

Ketchen (1953), while studying factors affecting the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, B.C., discovered an inverse correlation between year-class strength and water temperature at the time of pelagic life. By relating

drift currents with temperature conditions in the Strait, the possibility of high temperatures so accelerating development that the young fish metamorphosed prior to reaching appropriate rearing grounds was demonstrated (cf. C. J. Fish, 1927; Walford, 1938). This interesting speculation exemplifies a more subtle limiting effect of temperature in combination with a second environmental factor.

Profitable comparison can be made with another cold-blooded vertebrate, the frog, from studies by Moore (1949) on some of the physical factors affecting distribution and survival in the genus *Rana*. In correlating adaptive differences with environmental temperatures, some of the main divergence among the species occurred in embryonic temperature tolerance and rate of development. The latter was greater at lower temperatures for species with a more northern distribution. This highly significant work on *Rana* points up the lack of such knowledge among other poikilotherms. Among amphibia in general McFarland (1955) has commented that "the effect of temperature acclimation on amphibians has been studied but little; in fact in the entire class little is known about lethal temperature limits."

A study of the stages in thermal requirements during development in fishes is sorely needed.

TEMPERATURE AND ACTIVITY

Death from temperature intolerance marks the ultimate breakdown in the organization of the individual. However, it is well recognized that feeding, resistance to disease, successful reproduction, and sufficient activity to permit existence in the face of competition and predation are all necessary for the continued maintenance of the organism. Within a population, inability to maintain any one of these activities at moderately extreme temperatures may be as decisive to continued survival as more extreme temperatures are to immediate life. Donaldson and Foster (1941) reported that when sockeye salmon fingerlings were gradually raised from 17.2°C. to 25.6°C. over a period of a week they "refused to eat and the respiration rate became excessive." By lowering the temperature to 21.1°C. feeding commenced and the fish "were able to make a very slight increase in weight." Water temperatures in the range of 4°C. to 7°C. produced poor growth. At a temperature of approximately 10°C., growth and

food utilization were highest for the temperature conditions studied.

Adult salmon move inshore and upriver when maturing and spawn in freshwater streams. In doing so they must pass through water temperatures which may be far more extreme than those under which they finally spawn. F. F. Fish (1948) reported that during the summer of 1941 "the temperature of the Columbia River at Bonneville averaged 68.5°F. (20.3°C.). On July 20, 1941, the Columbia reached an all-time high temperature of 74.5°F. (23.6°C.)—hot water indeed for the blueback salmon (*Oncorhynchus nerka*), but a congenial temperature for certain of their microscopic enemies. One of these, the myxobacterium *Chondrococcus columnaris* is particularly lethal to blueback salmon." The great losses in these salmon, almost obliterating the 1941 run, were attributed to the combined effects of high temperature and bacterial infection.

If the lethal temperature were directly related to other aspects of temperature and survival, in a like manner throughout species, it would constitute a very convenient index for a measure of the limitation of species. Lethal limits and the distribution of animals in temperature zones on the earth's surface would be in direct proportion, where temperature was the restricting factor. Frequently, such relations are but poorly represented. The crucial question appears to be what activity is possible in the region of the lethal temperature. If the ability to be active were not seriously limited at temperatures approaching the lethal level, such vital activities as feeding, competing, and migrating would still be within the powers of the animal up to that temperature. Slight increases in the temperature tolerance of the species would increase the possibility for greater environmental experience, and consequently be of survival value. Conversely, where the activity of the animal was restricted in the region of its lethal temperature, an increase in tolerance without an increase in the scope for activity would confer comparatively little survival value.

The work of Fry (1947a, b; 1948) and of Graham (1949) illustrates the points of this proposition. Fry (1947a) has reported the active and standard metabolism of the bullhead (*Ameiurus nebulosus*) at various temperatures ranging from 2°C. to 35°C., and bordering on the ultimate upper lethal

temperature for this species (about 37°C.). The difference between the active and standard metabolic rates at any given temperature is taken to be a measure of the scope for activity, the lower level of metabolism being ascribed to the energy required to maintain the animal when inactive. In this species the scope for activity increases with increasing temperature over the complete biokinetic range. The bullhead seems limited only by its ultimate upper lethal temperature rather than by any loss in available energy for activity. The speckled trout, however, reaches a peak scope for activity at about 19°C. (Fry, 1947b; Graham, 1949). Increasing temperature above this level results in decreasing ability to be active, down to a relatively low scope when approaching the ultimate upper lethal temperature. The bullhead is quite understandably a successful fish in the high temperatures of shallow lakes and inshore reed beds, whereas the speckled trout, although capable of withstanding a temperature as high as 25°C., is not likely to succeed in this environment.

Activity has also been measured by the speed at which fish can swim steadily in a rotating chamber (Fry and Hart, 1948). A relation between this measure of activity and that from a difference in standard and active metabolic rates was established for the goldfish (Fry, 1947a; Fry and Hart, 1948). A most appropriate work in this field on salmonoids was that reported by Fry (1948) for two charrs, *Salvelinus namaycush* and *S. fontinalis*, and two trouts *Salmo gairdneri* and *S. trutta*. Yearling fish of the various species were compared with respect to scope for activity by both the above methods at temperatures ranging from 5°C. to 25°C. Fry (1948) commented that "although it is not certain that the difference between trouts and charrs has a phylogenetic basis, these two groups show a striking difference in their *swimming-rate* versus *temperature* curves." The trouts both appeared to be capable of increasing activity up to their ultimate upper lethal temperatures, whereas the charrs showed a reduction in activity as the temperature approached the lethal level.

If this relation of activity to temperature has survival value, cases in which similar or nearly similar lethal temperatures exist, accompanied by dissimilar peaks for maximum activity, might be expected to have different distributions according to temperature, under otherwise relatively

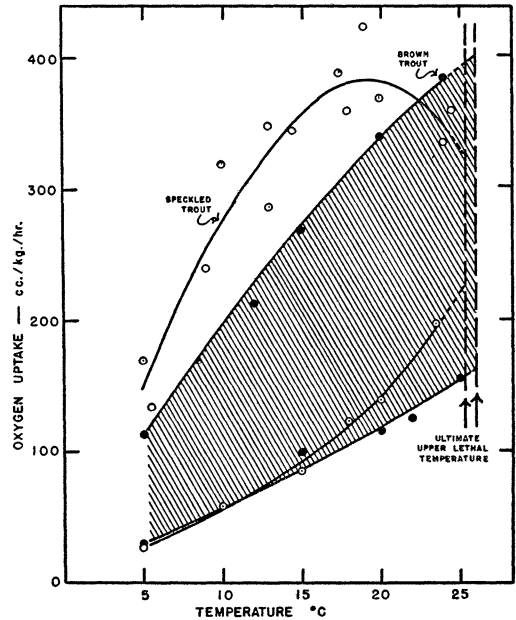


FIG. 3. THE RELATION BETWEEN TEMPERATURE AND METABOLISM FOR TWO SALMONIDS

The metabolism for speckled trout, *Salvelinus fontinalis*, and brown trout, *Salmo trutta*, has been measured as the active (upper) and standard (lower) levels of oxygen uptake when previously acclimated to each given temperature. (Data from Fry, 1948; Graham, 1949).

similar habitat conditions. The case of the brown trout and speckled trout appears to fall in this category (Fig. 3). King (1943) recorded that the brook or speckled trout is "considered a 'head-water' form and usually occurs in the upper stretches of trout streams," whereas the brown trout occupies "a position in the stream as a rule below that of the brook trout, but usually with an overlapping of ranges." Such a relation is supported by the work of Holton (1953). On the basis of their temperature-activity relations this is what might be expected. The brown trout shows a greater scope for activity at higher temperatures than does the speckled trout. The apparent support which these observations provide for the activity hypothesis cannot be pressed in any more serious form. The complexity of the problem may be judged by the diversity of opinions on trout distribution expressed in the literature which King (1943) has summarized most appropriately.

PREFERRED TEMPERATURES

The congregation of fish within a segment of the thermal range available to them has been re-

peatedly observed, both in nature (Dendy, 1945) and in the laboratory (Doudoroff, 1938; Sullivan, 1949; Sullivan and Fisher, 1953). Within the laboratory it is possible to eliminate many of the multiple factors of the natural environment (gradients of light, of gas and chemical content, of food and predator abundance) and to determine a *preferred temperature*. Like the lethal temperature and the temperature for optimum activity, the preferred temperature is subject to change through acclimation. Fry (1947a) has further indicated that a *final preferendum* may be established, where the preferred temperature equals the acclimation temperature.

The recognition of an ability among fish to perceive and select a limited thermal range has found significance in its relation to temperatures for optimum activity. In the goldfish, Fry and Hart (1948) noted that the final preferendum and the optimum temperature for cruising speed corresponded closely. Fisher and Elson (1950), using an electrical stimulus, measured the length of the initial dart made by speckled trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) parr at various temperatures. The maximum response occurred in the region of the preferred temperature, for the level of temperature acclimation of their samples.

Whatever the mechanism or process of temperature selection may be, the survival value of moving progressively into thermal conditions which offer a maximum expression for activity is most apparent. It is interesting to note that speckled trout are not usually found at temperatures exceeding 19°C., which is the upper limit of their preferred range, although considerably below their upper lethal level.

Doudoroff (1938) concluded from experiments with the marine fish *Girella nigricans* that the temperatures most frequently selected (26–27°C.) were not in keeping with the temperatures of their normal habitat (mean surface temperature of 20.8°C.). This apparent discrepancy may be attributed in part to the phenomenon of summation in acclimation, previously referred to for the bullhead (Brett, 1944, 1946), in which the field collections showed an acclimation to the maximum rather than to the mean temperatures of the environment. From Doudoroff's data, the final preferendum lies between 23° and 24°C., in agreement with the highest mean monthly record of 23.6°C.

DIRECTIVE FACTOR

The laboratory study of preferred temperatures reveals a considerable degree of insensitivity to temperature. The range for a preferred temperature observed among young Pacific salmon frequently amounted to eight Centigrade degrees (Brett, 1952). This would hardly convince the ecologist that temperature could act as a directive factor for the relatively precise migrations of at least one of the species (*Oncorhynchus nerka*). Yet their exodus from lakes has been shown to correlate significantly with rising spring temperatures (Foerster, 1937). Kennedy (1940) discovered a temperature relation between the movement of lake trout from a shallow lake, as it warmed in spring, to a deeper adjoining lake. In Lake Oredon, Jammes (1931) observed that the vertical distribution of trout was related to temperature, their position being apparently defined by that of the 12°C. isotherm. In the ocean, the spring movements of Atlantic mackerel (Sette, 1950) "appear to be spawning migrations in which temperature limits the northerly progress" regardless of feeding conditions.

It is also relevant to note the delicate sense of temperature perception displayed by *Jenkinsia lamprotaenia*. Breder (1951) observed schools of this species to avoid consistently a temperature of 30°C., although moving freely in a temperature of 29.0 to 29.5°C. and capable of withstanding 35°C.

Using the method of conditioned responses, Bull (1936) was able to demonstrate particularly fine temperature discrimination in a wide variety of species. Responses were obtained for temperature increases as small as 0.03 to 0.10°C. A minimum difference of 0.5°C. was required to produce an unconditioned orientation response in two species of *Pomolobus*, the alewife and the glut herring (Collins, 1952).

Critical temperature conditions have been ascribed to maturation and spawning in some fish. Bullough (1939) discovered that in conjunction with long daily periods of artificial light a temperature of 17°C. brought on maturation of the gonads in the minnow *Phoxinus laevis*. A temperature of 17°C. alone was found sufficient to induce completion of spermatogenesis in the stickleback, *Gasterosteus aculeatus* (Courrier, 1922). Craig-Bennett (1930) further noted that in the stickleback a rise in temperature during the spring was sufficient to change "potential maturity" to "functional maturity." Similarly, a rise in temperature

in the presence of vegetation is reported by Fabricius (1950) to release spawning activities in the pike (*Esox*), whereas the whitefish (*Coregonus*) require a lowering of water temperature with a particular character of bottom.

Thus it would seem that an inherent ability to perceive fine gradients of temperature is only exercised when called upon by some internal drive (possibly in some migrations) or by an environmental stress (possibly at higher temperatures). This would constitute a distinction between temperature as a directive factor and temperature as a preferendum. The preferred temperature does not exert such a "pressure" eliciting particular activities, but has a wider range of effectiveness governing the efficiency of performance of the fish.

SUMMARY

Among aquatic gill-respiring vertebrates there is no escape from environmental temperature. Tissue temperature and environmental temperature are constantly equilibrated at the gill surfaces.

Although the thermal requirements for fish have been seen to fall in a number of categories, the fundamental requirement can be restated—an *external* temperature best suited to the *internal* tissues. The tissues themselves are functionally adapted to a wide thermal tolerance, which is bounded by lethal limits and shows great diversity between species.

In general, cold-water fishes have a lower level of thermal tolerance than inhabitants of warmer waters.

Through reversible acclimation, which is more rapid for a rising temperature than for a falling

temperature, the degree of tolerance and the activity range is variously extended among species. A slow rate of *decrease* in environmental temperature is of greater importance for maintaining life than a slow rate of *increase*.

The combined information concerning lethal temperature and temperature permitting maximum activity, at all stages of development, is necessary for an interpretation of temperature in terms of survival value. Where high temperature does not limit activity, lethal levels can be expected to be a prominent environmental factor in setting the limits of distribution.

The scope for activity of cold-water fishes finds maximum expression at moderately low temperatures, which appear to be those frequented by the fish as preferred temperatures.

A potential for delicate discrimination of temperature differences among diverse species of fish is probably only exercised under particular environmental conditions.

Temperature, then, may act in the capacity of a lethal factor; it constantly conditions the fish through acclimation while governing the scope for metabolic rate; performance is best in the region of the preferred temperature; and a sensitivity to small gradients of temperature may act as a directive factor. Undoubtedly, the role of temperature among fish is a multiple one.

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