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EFFECTS OF THE ENVIRONMENT
ON ANIMAL ACTIVITY

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ON ANIMAL ACTIVITY

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CONTENTS

	PAGE
Introduction	5
Lethal Factors	11
Masking Factors	22
Directive Factors	22
Controlling Factors	26
Limiting Factors	41
Accessory Factors	52
Recapitulation	55
Literature Cited	60

EFFECTS OF THE ENVIRONMENT ON ANIMAL ACTIVITY

INTRODUCTION

In the ages that life has existed upon this planet adaptation has proceeded until now some particular form is able to live under almost any combination of physical and chemical conditions to be found in the environment. This phenomenon of the diversity of living organisms claims a great deal of the study which comprises the science of biology. Morphology describes the manifold structures of organisms, taxonomy classifies them according to these structures, embryology outlines the development through which each passes, genetics relates the characteristics of one generation to those of the next. The branches of the science which deal mainly with the variety of life are concerned largely with the study of form, either by observation or by experiment, but these studies of form are interpreted in light of function. By and large the functions that are of primary interest are those activities that enable the animal to cope with either its inanimate environment or its fellow organisms.

The study of form and the interpretation of function from this study have been exceedingly fruitful efforts. Indeed although no biologist would accept cadavre as the species, neither probably is there any biologist who would entirely accept a species record without the cadavre in his hand, or the more convenient portions of it safely deposited in some museum. There is no doubt then, while our concept of the species can be crystallized by the phrase that it is "out of heredity by environment," which is surely a functional concept, so convenient is our present method that our descriptions of species contain virtually nothing but a catalogue of diagnostic portions of anatomy.

However, we have now in many cases, particularly in the study of infraspecific relationships, nearly reached the end of our morphological tether, and for some years past, more and more effort has been devoted to the physiological description of animals. At the present time, in spite of the increasing activity in this field, there does not appear to be any unified approach to this problem. Nor does it appear that such an approach can be borrowed in its entirety from

ACKNOWLEDGEMENTS

In attaining the point of view presented here I have absorbed much, consciously and unconsciously, from my colleagues and teachers that will not be given specific reference in the text. In particular I should like to acknowledge the profit and pleasure that I have enjoyed through association with my colleagues, Professor and Mrs. E. C. Black. Little of the work that we have done together is referred to here but it all has played a major part in leading me to this analysis of the situation. I am also indebted to them and to Professor R. R. Langford for critical readings of the manuscript.

This work has been carried out in the Ontario Fisheries Research Laboratory of the Department of Zoology, University of Toronto. My thanks are due to the Director of the Laboratory, Professor W. J. K. Harkness, and to the Head of the Department, Professor E. M. Walker, for their full support.

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those branches of the science that are devoted exclusively to the study of function, for the purely physiological approach has been, and rightly so, to analyse the processes that go on within the organism, rather than to classify the organism in the light of the activities which it exhibits.

Since there does not appear to be a ready-made approach to the physiological description of organisms that may be taken over from the physiologists, an attempt has been made here to provide the basis for one. To provide this foundation, the inanimate factors of the environment have been classified according to their relation to the metabolism of the organism and hence to its activity, and the consequences of these relationships have been treated with particular reference to one group of organisms, the fish.

The Concept of Activity

The study of the functioning of organisms embraces two subdivisions which do not always appear to have been clearly defined although they are in general universally recognized. These are, in everyday language, how the organism works and what the organism does. The first of these groups of functions we define as metabolism. Hence the term metabolism embraces those processes which supply the energy whereby the organism continues to exist and to gain energy with which to respond to its surroundings. The metabolic processes are of course all those thousand and one reactions that go on within the living organism and are the dynamic, as protoplasm is the physical, basis of life. It is not worth while enumerating any of them as examples, but one might here introduce the analogy of the machine. You might say that the combustion of gasoline and the production of the electric spark are the metabolic processes of the motor car.

Following common practice we shall term those things which the organism does, activities. Thus activities are such processes as running and fighting and other manifestations of the energy that is released by metabolism. These manifestations are not all mechanical, growth is an activity and so is excretion. The distinction between activity and metabolism may perhaps appear to be laboured here, but much confusion in thought exists in the literature. The confusion between activity and metabolism has of

course not arisen from misnaming the activities but from considering measures of activity as equivalent to measures of metabolism. To return to the analogy of the machine, the activity of the motor car is motion. The activity of the machine is the result of its integrated metabolism: so also is the activity of the animal.

The idea of activity as distinct from metabolism and the concept that the environment influences activity by acting on metabolism will be the theme of practically all the ensuing discussion.

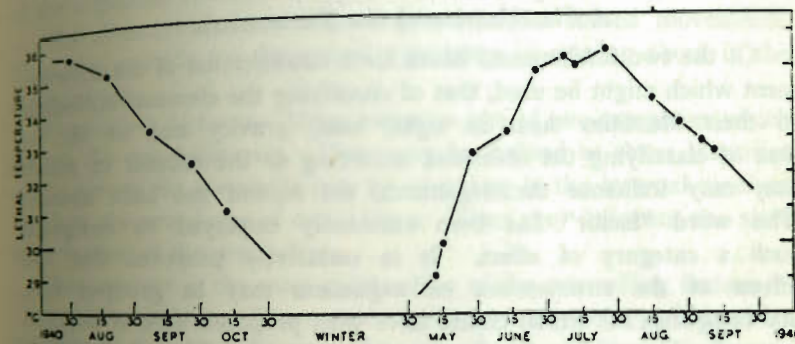


FIGURE 1.—Variation in the upper lethal temperature of the fish *Ameiurus nebulosus* in lake Opeongo, Ontario, 1940 and 1941. (Brett 1944, figure 3.) The points indicate temperatures which are fatal to 50 per cent of the sample during an exposure of 12 hours.

Two principles concerning activities, which have long been recognized but not always applied in investigation, may be stated here. They both follow from the fact that activities are the result of organized metabolism. The first of these is that since activity of the animal as a whole is the result of integrated metabolism, it follows that the metabolism from which the activity results is not the total metabolism of the organism at that time, but is the difference between the total metabolism and the metabolism required for the organism's integration and for the support of the ancillary activities which enable it to carry out the activity under consideration.

The second principle is that previous experience of the organism in relation to the factor of the environment under consideration must always be taken into account. When studying the organism as a

whole some assessment of this previous experience will always be required before any measurement will have a precise meaning. As an example, the familiar and sometimes great difference in the upper lethal limit of temperature which is to be found in animals of the same species with different thermal histories may be cited. An illustration of such variation is given in figure 1 where the seasonal change in the upper lethal temperature of bullheads taken from Lake Opeongo, Ontario, is shown.

A Classification of the Environment

Of the two fundamental bases for a classification of the environment which might be used, that of classifying the elements according to their identities such as light, heat, gravity and so on, or that of classifying the identities according to the manner in which they may influence the organisms, the second has been chosen. The word "factor" has been commonly employed to designate such a category of effect. It is tentatively proposed that the effects of the environment on organisms may be grouped into six categories for which names have been proposed here or adopted from the literature. These categories are defined and discussed briefly below.

Lethal factors:—An environmental identity acts as a lethal factor when its effect is to destroy the integration of the organism.

The lethal effect of any identity may be separated into two components, (a) *the incipient lethal level*, that level of the identity concerned beyond which the organism can no longer live for an indefinite period of time, and (b) *the effective time*, the period of time required to bring about a lethal effect at a given level of the identity beyond the incipient lethal level.

The effect on the organism as measured by both the incipient lethal level and by the effective time will depend on such previous experience of the organism as is significant to the measurement in question, and such measurements require a description of this significant history before they are valid. Such a definition may be given in terms of the level of the identity concerned to which the organism is completely acclimated.

Masking factors:—A masking factor is one which prevents a

second identity from operating on the organism to the extent that it would if the masking factor were not present.

The effect of evaporation rate on the body temperature of the terrestrial animals is a familiar example of the operation of a masking factor. Here the degree of humidity and air movement are masking factors, modifying as they do the effect of the dry bulb temperature on the animal.

Directive factors:—These allow or require a response on the part of the organism directed in some relation to a gradient of the factor. The directive factors elicit the well-known forced movements. They also provide for the animal's guidance in moving about in the environment.

Controlling factors:—These comprise one of two categories which govern the metabolic rate. They may be defined as those identities which govern the metabolic rate by operating in the internal medium which is the actual site of metabolism. Thus they influence the state of activation of the metabolites.

Temperature is the most outstanding of the controlling factors.

Limiting factors:—These make up the second category of identities that govern the metabolic rate. The term is derived from Blackman's (1905) category of "limiting factors" and it is applied here in the sense in which he used it except that we are excluding those factors that we are designating as controlling factors.

The limiting factors may be defined as those identities which govern the metabolic rate by virtue of their operation within the metabolic chain.

A zoological example of the classical Blackmanian scheme of the operation of limiting factors is to be found in Pütter's (1914) work on the limiting effect of various oxygen tensions on the response of the cutaneous respiration rate in the frog to increase in temperature. This example is illustrated in figure 2. Here it will be seen that when the oxygen tension in the water surrounding the animal was from 80-140 mm. Hg. the rate of uptake of oxygen by the skin increased with increasing temperature up to about 14°C. Beyond 14°C. no further increase in rate of oxygen uptake accompanied an increase in temperature when the oxygen tension was held to the limits mentioned. Similar plateaus of rate of oxygen uptake are reached at various higher temperatures at higher tensions of oxygen. When such a

plateau is reached oxygen is said to be a limiting factor, since increasing other identities does not increase the metabolic rate.

Accessory factors:—An accessory factor is one which imposes a metabolic load upon the organism in excess of the rate to which the organism is confined by the factor which is governing the over-all metabolic rate. This combination results in the death of the organism.

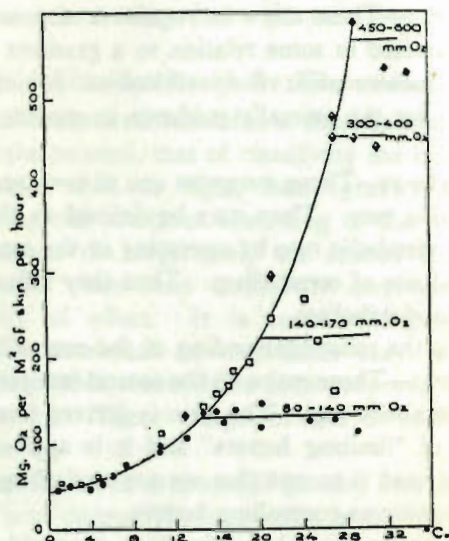


FIGURE 2.—The effect of certain tensions of dissolved oxygen on the relation of cutaneous respiration in the frog to temperature. Data from Pütter (1914).

An example of such a combination to bring about a lethal effect has been given recently by Doudoroff (1945) who shows that certain low temperatures in themselves are not fatal to marine fish. However, they do prevent the animal from maintaining its osmotic balance in its hypertonic medium and the consequence is that death results. Here salinity is imposing the load and acting as an accessory factor.

Concluding Remarks

A particular environmental identity, temperature for example, may at different times act under a different category of the classification presented above and commonly does so. What category a

particular identity acts under at a particular time will depend on the levels of the identity under consideration and of all the other identities in the environment, and of course on the organism concerned. These details will be taken up in the following sections for each category in turn, with particular reference to their place in the physiological description of species.

LETHAL FACTORS

The discussion of lethal factors will be illustrated chiefly by reference to the lethal effects of high temperature. It may be remarked at the outset that although a great deal of investigation has been carried on in which the chief concern of the investigator has been the assessment of the lethal limits of temperature for a given organism, very few of the results of this work can be accepted as being more than preliminary. In general the greatest gap in these data is an almost complete lack of any record of the thermal history of the organisms on which the lethal limits were determined. In this respect however, workers using fish have been least remiss. This lack of what in those cases for which it has been determined, is extremely pertinent information, renders useless for all but the most general conclusions, most of the values given in the literature.

An example of the tremendous effect of the thermal history has already been given for fish in figure 1. A second example, relating to the invertebrates might also be quoted with profit. Horstadius (1925) showed that the temperature limits for the normal development of eggs of the echinoderm, *Paracentrotus lividus*, acclimated to winter temperatures (13°C.) were approximately 8°C. and 23°C. When acclimated to summer conditions (26°C.), the limits were 16°C. and 29°C. Thus here a thirteen degree change in the mean temperature at which the parents were living brought about a change of some six degrees in the upper lethal limit of temperature for normal development of the eggs, and of eight degrees in the lower lethal limit. Changes of this order are apparently often to be expected.

Methods of Determining the Lethal Limits of Temperature

There have been two general experimental procedures followed for the assessment of the lethal limits of temperature. One method has been to warm or cool the organism at a given constant rate until it

died. This method is rapid and convenient and requires little in the way of apparatus. In the past it has yielded valuable results in broad preliminary comparisons. (Vernon, 1899, Huntsman and Sparks 1924, Battle 1926). Unfortunately it is not an ideal analytical method since the measurement itself involves two variables, time and temperature; and as will be shown later, analysis by the second method will allow prediction of results obtained by this one.

The second general experimental method is to maintain thermostats at various constant temperatures in which samples are introduced and the time to death noted. Results obtained in experiments of this type have been expressed in two ways. Some workers have plotted time mortality curves (Bliss 1937), others have used the dosage mortality method (Bliss 1935). For the statistical details involved in these calculations the original papers of Bliss and that of de Beer (1945) should be consulted. However, with a complete set of data one can calculate both the time to death at any lethal level of temperature (time mortality), and the temperature required to bring about death in any prescribed interval of time (dosage mortality). Both statistics appear to be necessary for a description of the lethal effect of temperature complete enough to cover the ecological conditions which the species may encounter and still survive.

We have already stated (page 8) that the effect of a lethal factor may be separated into two components, (a) the incipient lethal level, that level beyond which the organism can no longer live for an indefinite period of time, and (b) the effective time, the period of time required to bring about a lethal effect at a given level of the identity beyond the incipient lethal level. We should now add that as far as the organism is concerned, the incipient lethal level divides the range of experience of that identity, within which it is possible for the organism to exist at all, into two zones. Within the upper and lower incipient lethal levels there is what may be designated as the *zone of tolerance* in which the animal will never die from the effects of that particular identity alone. Beyond the incipient lethal levels there lies a *zone of resistance* in which the animal will ultimately succumb to the effects of the identity in question, but in which it can resist this lethal effect for a period of time which is a function of the level of the identity. Let us now consider how these two zones can be mapped

out and described by convenient indices when temperature is the lethal factor. A prerequisite to this description is that it must provide for all possible thermal experiences to which the organism can be subjected and survive.

Thermal Tolerance

The requirement with which the preceding section was ended can be fulfilled only by means of a quantitative description of the manner in which the history of the organism affects its ability to exist over a range of levels of a given factor. In the case of temperature, the method which in light of the information at hand appears to be adequate for fish and no doubt could be applied to many other groups of animals with equal success, is to maintain the animals at various constant temperatures for periods of time sufficient to ensure that they are acclimated to these temperatures, and under conditions that ensure no other factor is exerting any significant environmental stress upon them. The importance of guarding against stress from other sources is clearly illustrated by Brett's (1946) experiment on the influence of oxygen tension on the rate of thermal adaptation of the bullhead the results of which are illustrated in figure 3.

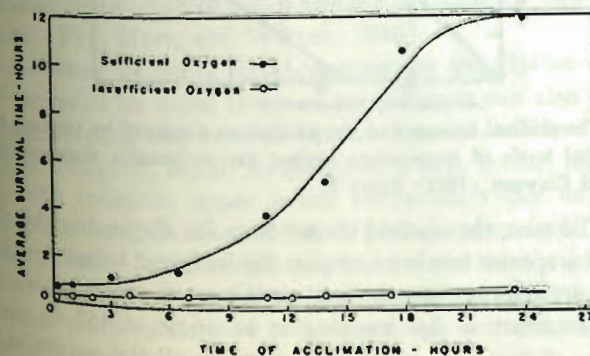


FIGURE 3.—The influence of oxygen tension on the rate of thermal acclimation in the bullhead, *Ameiurus nebulosus*. Brett (1946) figure 6. (1) Sufficient oxygen. The average survival time at 35.5°C. when taken from 20°C. and put at 28°C. (2) Insufficient oxygen. The average survival time at 35.0°C. when taken from 17°C. and put at 27°C.

Samples of fish from the acclimation tanks are then exposed to various constant temperatures and the time to death recorded either for each individual or as within a given interval of time. For the present purpose we shall define the incipient lethal temperature as that temperature beyond which 50 per cent of the population can no longer live for an indefinite period of time.

When these upper and lower limits to the thermal tolerance of the organism have been determined for a series of levels of acclimation temperatures they may be plotted in a manner which allows the whole thermal tolerance of the animal to be displayed. A graph of this type is given in figure 4 which illustrates the thermal tolerance of the goldfish.

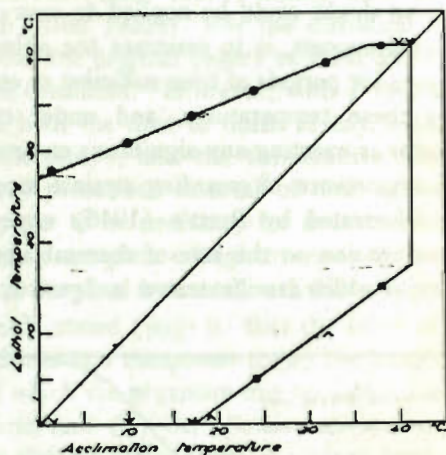


FIGURE 4.—The thermal tolerance of the goldfish as displayed by plotting the incipient lethal levels of temperature against the acclimation temperature. Fry, Brett and Clawson (1942) figure 2.

As will be seen, the method chosen here for displaying the thermal tolerance of a species has been to plot the incipient lethal temperature against the acclimation temperature on a square graph which has an additional construction line running at an angle of 45° to the axes. The purpose of this line, which runs through all the points at which measurements along each axis have equal values, is to provide a ready indication of where the lethal temperature and the acclimation temperature are the same. Thus the point to the right where the upper incipient lethal temperature reaches this 45° -degree line marks the end

of acclimation in that direction and a perpendicular can be dropped from there which terminates the line describing the relation of the lower lethal temperature to the acclimation temperature. The complement would be true of the point to the left where the lower lethal line cuts the 45° -degree line. In the case of the goldfish, however, as would be the case for many other species also, such a coincidence of the lower lethal with the acclimation temperature does not occur, for water changes its state above the ultimate lower incipient lethal temperature and is no longer a suitable medium for the animal concerned. For this reason both the upper and the lower lethal temperature-acclimation temperature curves terminate to the left at the axes.

The two lethal lines, together with portions of the axes and the perpendicular dropped from the point where the upper lethal coincides with the acclimation temperature, enclose an area which contains all the possibilities, thermally speaking, which the animal in question can tolerate indefinitely. This area may be called the thermal tolerance and can be determined quantitatively. It is no longer necessary to cling to the qualitative terms "stenothermal" and "eurythermal" for those species for which this determination can be made. The value for the thermal tolerance of the goldfish on the Centigrade scale is 1220 units, the units being square degrees. For the bullhead the thermal tolerance is 1160 units (Brett 1944) and for yearling speckled trout, *Salvelinus fontinalis*, a value of 625 units has been found (Fry, Hart, and Walker, 1946).

Various other values of significance in the description of a population in terms of its lethal limits of temperature can also be derived from tolerance diagrams such as that in figure 4. There is an ultimate upper incipient lethal temperature which is the highest level to which the incipient upper lethal temperature can be raised by thermal adaptation. In the goldfish this temperature is 41°C . There is also an ultimate lower incipient lethal temperature, which has not been determined for the goldfish, and there is a minimum incipient upper lethal temperature and correspondingly a maximum incipient lower lethal temperature.

Thermal Resistance

The description of the thermal tolerance of a species, complete though it may be, and neat as it is for the purposes of physiological

description, does not entirely describe the relation of the species to its environment in terms of temperature as a lethal factor. The animal can exist, often for substantial periods of time, at a temperature level beyond the zone of tolerance, and may frequently do so, particularly during diurnal fluctuations. Thus the zone of resistance which lies beyond the zone of tolerance also requires evaluation. The effective times give the necessary information with which to describe the zone of resistance.

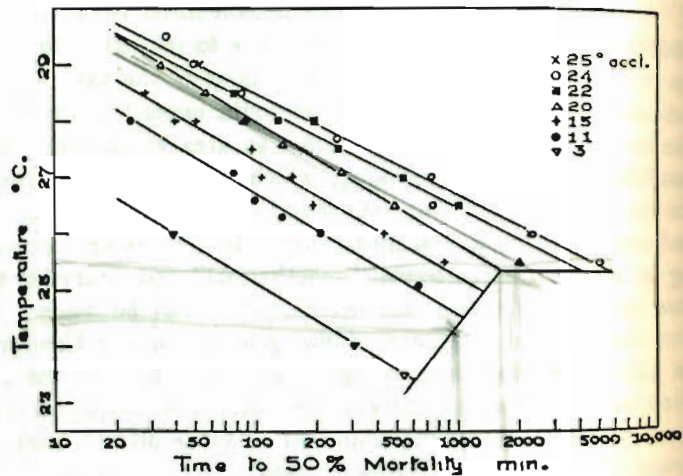


FIGURE 5.—The time to 50 per cent mortality at various lethal levels of temperature for speckled trout, *Salvelinus fontinalis*, acclimated to various temperatures. From Fry, Hart and Walker, (1946) figure 2.

The first step in the determination of the thermal resistance is to determine the effective times for a series of lethal levels of temperature for subjects adapted to various temperatures over their biokinetic range. The results of such a series of determinations on the speckled trout are plotted in figure 5. A feature of figure 5 that may be puzzling on first inspection is that the resistance lines are terminated abruptly to the right by two boundary lines. These lines pass through the upper incipient lethal temperatures for each respective level of acclimation and thus the resistance lines do not have meaning beyond these points, for 50 per cent mortality never results from temperatures below these regardless of the length of exposure.

Now, for any given level of acclimation a measure of the zone of resistance expressed as a single numerical value, can be obtained by finding the area under the effective time-temperature line, from a time of say one minute up to the time required to measure the incipient upper lethal temperature. For the 3°C. acclimation level in figure 5 the time where the line describing the relation of the effective time to temperature meets the line joining the incipient lethal temperatures is 600 minutes. Knowing the formula for the line (Fry, Hart, and Walker 1946) the area under this curve can be summed from time = 1 minute to time = 600 minutes, and comes to a value of 546 degree minutes. The mathematical details have been suppressed here since we are concerned only with the general case. A series of such values can be found for areas under a series of such curves, each curve being the result of experiments on samples of a particular thermal history. These values can then be plotted

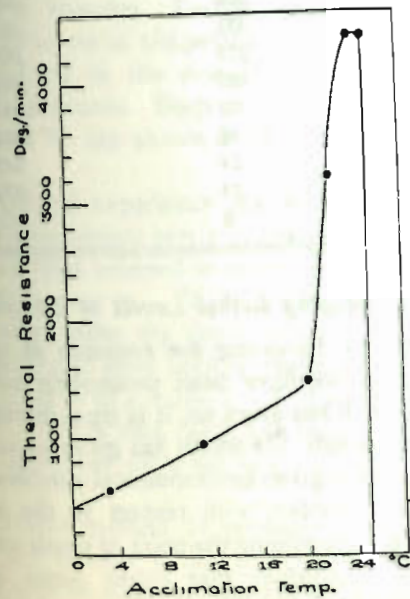


FIGURE 6.—A method of displaying thermal resistance as illustrated by the data for the speckled trout shown in figure 5. The area under the curve from 0°C. to 25.3°C. is 3.6×10^4 deg.² min.

against acclimation temperature and the area under this curve summed up to give a general over-all picture of the thermal resistance of the species. Such a curve is plotted in figure 6 for the speckled trout, each point shown being the area under one of the curves in figure 5.

The quantitative expression of thermal resistance proposed above is not nearly as meaningful as the expression for the thermal tolerance, but it has its value as a means of comparison. Species with a high value for thermal tolerance may have quite a low value for thermal resistance, or the opposite may be the case.

TABLE 1. The thermal resistance of yearling speckled trout acclimated to 11°C. Data from formula in Fry, Hart and Walker, 1946.

Temperature C°.	Resistance time minutes	Minute rate of mortification
25.0	639	.0016
25.5	371	.0027
26.0	215	.0046
26.5	125	.0080
27.0	72	.0139
27.5	42	.0238
28.0	24	.0416
28.5	14	.0714
29.0	8	.1250

Death in Changing Lethal Levels of Temperature

Up to this point in discussing the response of animals to lethal levels of temperature we have been proceeding towards a rather artificial endpoint which has given us, it is true, numerical indices for the classification of animals, but which has given us no precise understanding of the effect of a given environmental condition on the organism. The ecological problem with respect to the lethal effects of temperature is that of determining the point of death under any pattern of time-temperature conditions that might occur in nature. The problem has been solved in the following way and tested experimentally on such diverse organisms as starfish larvae (Jacobs 1919) and speckled trout (Fry, Hart and Walker 1946).

If you begin with the assumption that the rate of dying at a given constant lethal level of temperature is linear with respect to time, you can calculate a *minute rate of mortification* for each such level. This minute rate is the reciprocal of the effective time in minutes. Thus if the effective time brings about the death of the organism in 100 minutes the minute rate of mortification would be 0.01, and so on. Table 1 lists the minute rate of mortification at different lethal levels of temperature for yearling speckled trout acclimated to 11°C.

It follows that if the assumption made above holds, the time of death in changing lethal temperatures will be the point at which all the fractions of dying at the various temperatures add up to unity. To calculate this point when the time-temperature curve follows no particular formula, a graphical method may be employed. First mark off one axis of a piece of arithmetic paper in intervals from zero to one to represent the minute rate of mortification (or from zero to one hundred to represent the percentage minute rate). The other axis is marked off in minutes. Distances representing the mortification rate for lethal levels of temperature at degree and half-degree intervals are marked off on the mortification scale and assigned to the appropriate temperatures. Such scales, appropriate for speckled trout acclimated to 11°C. are shown in figure 7, and are plotted from the data in table 1.

For a given thermal experience the time-temperature curve is drawn through the appropriate levels by reference to the temperature scale. If this curve is then referred to the reciprocal scale, what results is a time-mortification curve. To determine at what point death would occur, the area under the curve is summed progressively by reference to the reciprocal scale until it reaches a value equivalent to total mortification, that is to a value of 100 if mortification is expressed in percentages. When this point has been reached the thermal experience would have been sufficient to bring about the death of the animal.

An example of this method of estimation is given in figure 7 which illustrates the results of an experiment performed on the speckled trout. It will be seen that there is almost perfect agreement between theory and experiment in this example. The area under the curve amounted to 101 at the time that death occurred, which is very close to the 100 required by theory.

It can now be seen, since the experimental method of determining the lethal effects of temperature by slow heating is just a special case of acclimation and dying under varying temperature conditions, how data obtained by this method can be interpreted, insofar as lethal effects are concerned, only by results obtained by the method of exposure to constant temperatures.

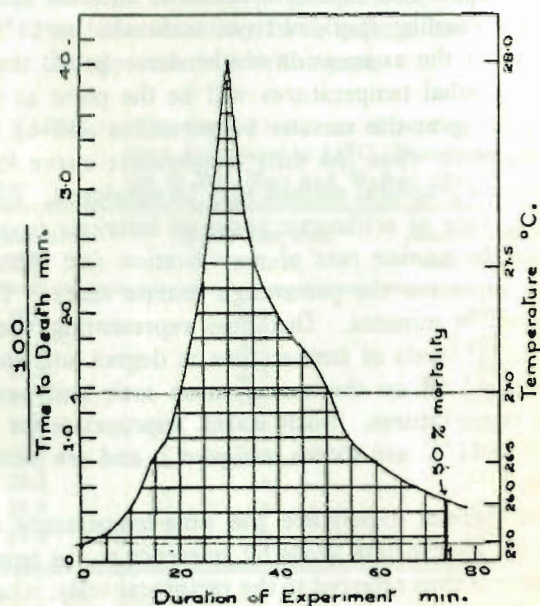


FIGURE 7.—Estimation of the thermal death point under continuously changing temperature conditions. The experiment illustrated was performed on yearling *Salvelinus fontinalis* acclimated to 11°C. Each square indicated under the curve represents 1% (0.2 x 5) of the theoretical mortification. From Fry, Hart and Walker (1946) figure 6.

The Rate of Thermal Acclimation

The perfection of the experiment illustrated in figure 7 should not be allowed to obscure the fact that it was designed to demonstrate only a single specific point, namely the summation of the thermal experience at temperatures above the incipient upper lethal temperature. To this end heating was begun at 25°C., a temperature above the incipient lethal level for speckled trout acclimated to 11°C. If

instead the heating had been started at 11°C. and carried on at the same rate, sufficient time would have elapsed before the zone of resistance was reached for further acclimation in the trout, which acclimate rapidly, and they would have survived for a substantially longer time at the higher temperatures.

The measurement of the rate of thermal acclimation may be said to be at present in the semi-quantitative stage. It is sufficiently advanced in order that some comparisons between species are possible, but there is as yet no information on any species complete enough to enable the acclimation level of its members to be estimated from a time-temperature curve describing their thermal history. Also, it has not been demonstrated whether thermal adaptation in all its manifestations proceeds simultaneously. Brett (1946) distinguishes between gain in heat tolerance and loss of cold tolerance as two processes that may possibly proceed at different rates.

It will be appreciated therefore that since the literature dealing with the rate of thermal acclimation does not yet contain any complete analysis of the problem, it will not be possible to carry the discussion to any completely satisfactory conclusion. For a review of the present situation as it pertains to fish the reader is referred to Brett (1946).

Concluding Remarks

We shall close the discussion of temperature as a lethal factor at this point. There appears to be hope that methods for the laboratory measurement of the effects of temperature as a lethal factor will soon be virtually perfected. The knowledge required for this assessment pertains to the extent of the zones of thermal resistance and thermal tolerance, to the influence of thermal adaptation on these characteristics and to the course and rate of thermal adaptation. Of these measurements all but the last appear to have been satisfactorily accomplished, and surely the last will soon be done also.

The example used for the discussion of lethal factors has been a somewhat narrow one. We have considered the fish almost exclusively. These organisms represent but a narrow class in a small phylum, and we have ignored the effects of any extensive resting stages such as are found in the insects. Moreover we have almost completely omitted discussion of the lower lethal limits of temperature,

and have considered the lethal effect of temperature in only one medium, water. However, it is hoped that the principles demonstrated within these narrow bounds while not all-embracing, will be of wide-spread application in relation to the lethal effects of other factors on a variety of other organisms.

MASKING FACTORS

The masking factors were defined as those factors which prevent a second identity from operating on the organism to the extent that it would if the masking factor were not present, and the familiar effect of the evaporation rate on the body temperature of terrestrial animals was cited as an example of this type of factor.

The subject of masking factors is a very important and far-reaching one for it may be contended, if one takes the view that the organism is fundamentally an organized section of the environment, that any stability the animal may have attained in its internal milieu in the face of the varying conditions in the environment has come about through the exploitation of masking factors. If such is the case it is evident that the wisest course to adopt in the present outline is to say as little as possible about the matter.

Therefore we shall consider only one generalization. That is that a masking factor would appear rarely to operate *per se*. In the case of humidity for example, only in exceptional cases would the animal be able to take more than a fleeting advantage of the cooling effect afforded by the rapid evaporation of water from its surface when in a dry and breezy atmosphere, without drawing on some internal supply for the water. Thus the advantages conferred on the organism by the operation of a masking factor can usually be gained only by expending some metabolism, or at least through the presence of some organization.

DIRECTIVE FACTORS

Directive factors are those factors which allow or require a metabolic response on the part of the organism directed in some relation to a gradient of the factor. Directive factors elicit the well-known forced movements but the definition also includes many more effects of the environment. It includes all the clues that the environment gives the animal by which it determines its own location and that of its fellow

organisms. Thus light is operating as a directive factor when an organism sees and moves towards its prey. The space devoted here to directive factors will be small, since other workers, and indeed another branch of science, psychology, give this subject ample definition and consideration.

It will have been concluded from the opening paragraph of this section that for any environmental identity to act as a directive factor it must be perceived by the organism. If there is no perception on the part of the organism it will not avoid even a lethal level of any identity. For man for example, there is much evidence placed every year before sundry coroner's juries that carbon monoxide does not act as a directive factor for that particular species.

Finally in a general reflection on the subject it must not be overlooked that in many cases we apply two special terms to the acclimation effect of a directive factor—those terms are learning and memory.

We shall confine our attention here to a consideration of one of the grosser manifestations of a directive factor which gives promise as a means of physiological classification. This is the measurement of the preferred temperature.

Preferred Temperatures

It is a well established fact that animals presented with a suitable range of temperatures in a restricted space will tend to congregate either at one end of that range or at some more or less definite temperature within it. It may be assumed that congregation at one end of such a range merely indicates that the range of temperature presented does not extend far enough in that direction. Thus in an infinite range of temperature there will be a region at which a given population will congregate with more or less precision given an opportunity to do so. This temperature has been most widely designated in English as the "preferred temperature" or the "preferendum,"

Measurement of the preferendum has usually been made by one of two general methods. In one a single individual at a time has been placed in a temperature gradient and its position noted at various consecutive intervals. In the other a group of individuals has been exposed to such a gradient and counts made of the distribution of these individuals over the various temperature levels at some

one or a series of later times. The preferendum has been expressed either as a modal temperature, a range containing say the middle 50 per cent of the total observations, or a mean selected temperature. A typical set of observations taken in determining the preferred temperature of fish is shown in figure 8.

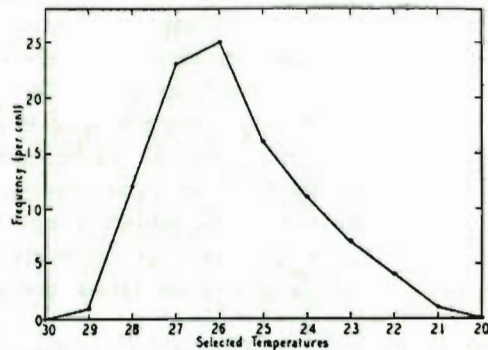


FIGURE 8.—Temperatures selected by *Girella nigricans* taken from current seasonal temperatures. From Doudoroff (1938). Reprinted from the *Biological Bulletin*.

The preferendum varies somewhat with the thermal history of the animal and any description of it must display this relation. A useful method of displaying the thermal preference of a population is to employ a square graph similar to that used in figure 4 to display the thermal tolerance. Such a graph is given in figure 9, in which the relation between the preferred temperature and the acclimation temperature is shown for two species of fish. An interesting and obvious feature of the preferendum is shown in figure 9. There is what may be termed a *final preferendum*, that is a temperature around which all individuals will ultimately congregate, regardless of their thermal experience before being placed in the gradient. The final preferendum is that temperature at which the preferred temperature is equal to the acclimation temperature. These points for *Girella nigricans* and *Carassius auratus* are indicated by circles on the graph. The final preferendum offers a convenient and meaningful index of the influence of temperature as a directive factor.

Some authors would object to the application of the word "mean-

ingful" above for there has been some question as to the ecological meaning of the preferendum. Doudoroff (1938) for example, mentions the tremendous difference in scale that there may be between the laboratory experiment and conditions in nature. He also points out that whereas the preferred temperature of *Girella nigricans* is 24-27°C. the animal lives and competes successfully in an environment in which the highest mean monthly temperature is about 21°C.

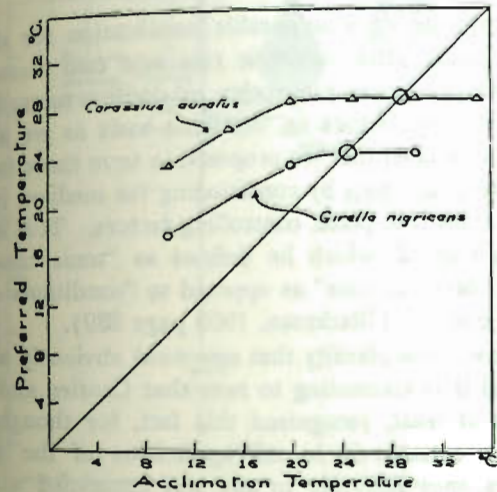


FIGURE 9.—The relation of the preferred temperature to the acclimation temperature in two species of fish. Data from Doudoroff (1938) and Fry (ms.).

While the evidence yet available concerning the relation of the preferendum to optima for activity is meagre, it is not all negative. Fisher and Elson (1940) point out that the optimum temperature for response to an electrical stimulus in the speckled trout found by Elson (1942) coincides with the preferred temperature. A similar correlation has been observed by Scott (ms.) in tadpoles (see also Fisher and Scott 1942, Workman and Fisher 1941). Fry and Hart (ms.) showed that the cruising speed of the goldfish reached a rather flat maximum in the region of the final preferendum but did not change greatly over the range from 20°C. to 30°C. (See figures 9 and 15 to make this comparison.) However, this was true only when the fish were thermally adapted to the temperatures at which the cruising

speeds were measured. In series where the cruising speeds were measured of fish without this previous adaptation there was no necessary relation to the preferendum. Nevertheless the very lack of such correspondence is of value to the goldfish for the response to the temperature gradient is such as to bring the animal into the zone in which it can be most active, when once it becomes acclimated.

CONTROLLING FACTORS

There appears to be considerable justification for dividing the factors which govern the metabolic rate into two classes. Indeed Blackman (1905) proposed just such a subdivision towards the end of his paper on limiting factors on the same basis as we are adopting here. It will be recalled that we proposed to term those factors which influence the metabolic rate by conditioning the medium in which the metabolic processes take place, controlling factors. This is equivalent to Blackman's class 2, which he defined as "tonic conditions that affect only the metabolic rate" as opposed to "conditions of supply of material or of energy" (Blackman, 1905 page 289).

Temperature is the identity that acts most obviously as a controlling factor, and it is interesting to note that Crozier and his school, by implication at least, recognized this fact, for though they used temperature so extensively in the application of the principle of limiting factors, they were not in any way concerned with temperature itself as a limiting factor. Their concern was with the effect of temperature on the chemical activity of some substance that acted as a limiting factor in the metabolic chain.

Other identities that come readily to mind as being capable of operating as controlling factors are salinity, hydrogen ion concentration and humidity insofar as it affects the concentration of protoplasm.

In this section we shall concern ourselves largely with the discussion of temperature as a controlling factor. Two general principles concerning controlling factors can be stated immediately. The first is that controlling factors operate so as to govern both the minimum metabolic rate and the maximum metabolic rate. The second is that a number of controlling factors may and do operate simultaneously. Both these characteristics of controlling factors distinguish them from the limiting factors.

Rules Relating Temperature to Metabolism and Activity

The several well known rules which have been formulated to describe the relation of temperature to the rate of metabolism or of activity have a well established position in the literature (e.g. Belehradek 1930, 1935) and will not be discussed here at any length. The most important of them are summarized in figure 10 which shows

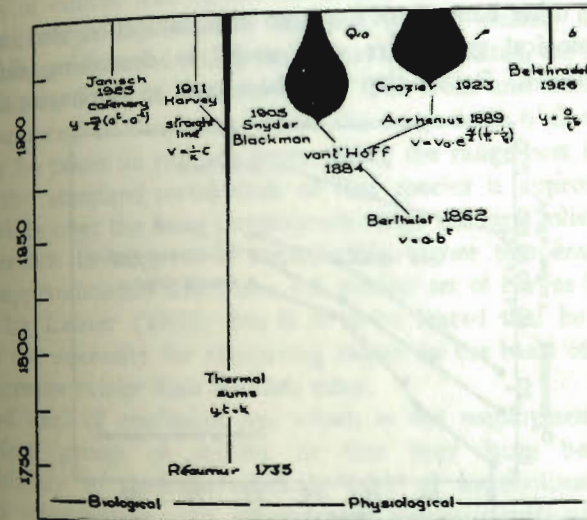


FIGURE 10.—The mathematical and historical relations of the major rules relating temperature to metabolism and activity. Constructed largely from the historical summary in Belehradek (1935) v —rate of metabolism or activity, y —time, t —temperature Centigrade, T —temperature absolute, all other symbols are constants.

their historical and mathematical relationships. As the grouping in figure 10 indicates, the various rules can be segregated into two divisions according to the purpose for which they have been used. These two groups may for convenience be called "biological" and "physiological." The biological group comprises those rules which have been used by biologists to describe the effect of temperature on various activities of organisms without reference to any underlying mechanism. Such a rule, for example, is the law of thermal sums. The rules which have been placed in the physiological group have,

on the other hand, been largely employed to describe the relation of temperature to the metabolic rate.

The suitability of formulae of the biological group as basis for a physiological index cannot be challenged except insofar as they fall short of being precisely quantitative. The rule of thermal sums for example is a useful field rule although it is well recognized that it does not hold exactly.

On the other hand there has been little indication that indices of the physiological group are very useful in describing differences between species. Rather they have been used to emphasize the simi-

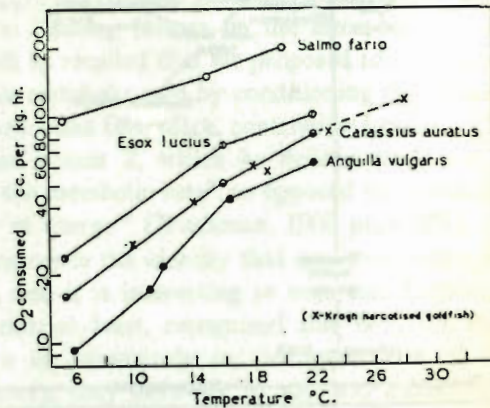


FIGURE 11.—The relation between temperature and oxygen consumption in four species of fish. Data from Gardner and King (1923) and Ege and Krogh (1914). Values from Ege and Krogh multiplied by 0.6 to bring them to the same level as the values of Gardner and King.

ilarity of response of widely dissimilar groups. The Q_{10} 's largely lie between 2 and 3, and when they do diverge it is usually considered that they do so because of the nature of the process and not of the species involved. Crozier (1925) felt that there were only relatively few μ values found during the assiduous labours of himself and his associates. Krogh (1914, 1941) has given a curve of standard metabolism in which he showed that a most diverse group of organisms gave the same proportionate response to changes in temperature.

While the use of a temperature index of the physiological group as an indication of differences between species is not very well advised,

since these indices measure slope only and not position, the slopes are not always as identical as Krogh's standard curve would indicate. Figure 11 illustrates four examples from one class of vertebrates, the fish, which have quite diverse slopes over the same temperature range. A direct comparison with Krogh's standard curve is given by the inclusion of his data for the goldfish adjusted to the appropriate level. This series of curves was chosen for another reason also, that is to illustrate a concept expressed by Barcroft (1934) namely that over a range of temperature for which the animal is best suited, the temperature-metabolism curve is relatively flat. The trout and the goldfish may be compared on this basis. Over the range from 6°C. to 20°C. which may be taken as roughly representing the range best suited to the trout the standard metabolism of that species is approximately doubled, while over the same temperature range the metabolism of the goldfish which is adapted to considerably higher temperatures, is increased approximately five times. A similar set of curves has been published by Leiner (1938) but it is to be feared that he did not appreciate the necessity for comparing slopes on the basis of relative rates of increase rather than absolute rates.

A good deal of confusion has arisen in the employment of the physiological group of indices in that they have been used indiscriminately to describe relations both of metabolism and of activity to temperature. In other words measurements of activity have been taken as reflecting quantitatively the metabolic rate. Except in those instances where the activity of an organ, for example the rate of the heart beat, may be taken as a reflection of the metabolic rate of the organism as a whole, there is no logical justification for assuming equivalence between measures of activity and metabolism.

This confusion of thought may perhaps be a relic of the chemical ancestry from which these ideas originally stemmed. It is true that any measure of a chemical reaction proceeding in a test tube will bear some ratio to all other measures that might be made of the same reaction. However, in such a test tube, no matter how complex the reaction, there is no integration at the organismal level, nor are any of the manifestations of the reaction, activities in the sense that we are using the term. It is to the machine and not to the test tube that we must look for an analogy with which to explain the relation of activity to temperature. This matter will be considered in the following section.

Temperature Optima

If there were such a thing as an optimum temperature for a given activity in organisms a very significant means of classification would of course be available and, one would imagine, be largely sought. However, due to the forceful clarification of the subject with regard

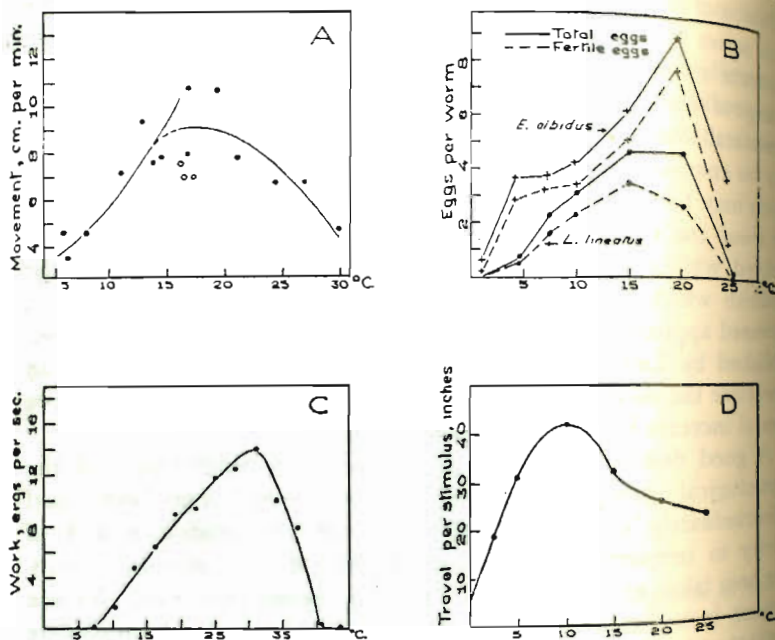


FIGURE 12.—Various temperature optima.

- Rate of locomotion of *Limax*. Crozier and Federighi (1924).
 - Fecundity of two species of worms. Reynoldson (1943).
 - Power output of oyster gills. Galtsoff (1927).
 - Response of the speckled trout to an electrical stimulus. Elson (1942).
- The graphs are reprinted with the permission of the various publishers.

to metabolism by Blackman (1905) and the pursuit of the analysis of mechanisms by physiologists ever since, the word "optimum" while not completely barred from the biologist's vocabulary, nevertheless can scarcely be uttered without some mumbled qualification. The subject is further confused because, when it has been employed, the term optimum has been used in two widely different senses. Sometimes

it has been taken to mean conditions that are best for the animal, whoever may be judge of that, at other times it has been applied to conditions under which an animal can perform a certain activity best as judged by objective measurements. Here we shall be concerned solely with the second meaning.

It is our purpose here to re-examine the case to see whether there are any circumstances under which the term optimum may be used in its own right as describing a level of a controlling factor at which a given activity of an animal can best be carried on, "best" being taken to mean accomplished at the highest level of the measurement taken.

Figure 12 shows a number of examples of temperature optima which fall within the meaning of the definition above. The processes in the examples in figure 12 are most diverse but it will be noted that they are all measures of activity and not of metabolism. Such a falling off of the rate of activity at the higher temperatures has of course often been noted and the commonest explanation is that it is due to some adverse effect of high temperature upon the rate of chemical action; this is the well known time factor (Blackman 1905). Belehradek (1935) indeed denies the possibility of any other explanation for he states (page 3) "When the upper biokinetic limit ('optimum') is passed, the velocity of biological reactions decreases to a complete stop, a phenomenon which is generally reversed on cooling."

It appears certain however, that not all of the evidence adduced to support the theory of thermal destruction points clearly to destruction and replacement of enzymes and also that the theory cannot be universally applied. For instance the cruising speed of the goldfish (figure 15) acclimated to 25°C. and tested at 35°C. will increase with continued exposure to the higher temperature although that temperature is above the optimum both for goldfish acclimated to 25°C. and for the general curve for the goldfish. However, without any means excluding the theory of thermal destruction, which certainly explains some cases in the literature, let us see if any other explanation can also be offered for temperature optima which does not conflict with all the well established knowledge concerning the relation between temperature and metabolism.

A mechanical analogy of the effect of a controlling factor on metabolism and activity is given in figure 13 which shows the relation

between speed of rotation, maximum power output, fuel consumption at full power, and fuel consumption under no load in the motor of a popular automobile manufactured in 1933. In this analogy the speed of rotation represents the level of the controlling factor, the power output, the activity, and the levels of fuel consumption the maximum and minimum metabolic rates.

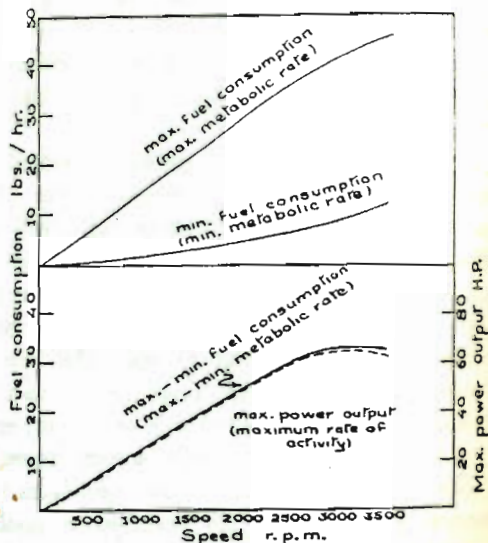


FIGURE 13.—A mechanical analogy of the effect of a controlling factor on metabolism and activity. The graph illustrates the relation between power output and fuel consumption in an automobile engine. These data were kindly supplied by members of the Department of Mechanical Engineering of the University of Toronto.

To maintain a motor under no external load at any given speed of rotation requires a certain minimum consumption of fuel. At the same speed of rotation it can consume fuel at a certain maximum rate. The difference between these two rates determines the power it can put out to perform external work. For example, at 1,000 r.p.m. the difference between the maximum and minimum levels of fuel consumption is 12 pounds per hour and the maximum power output is 24 h.p. Thus as the lower panel indicates, the correlation between power output and fuel consumption is with neither the maximum nor

the minimum rate but with the difference between the two. If the lesson of this analogy is applied to the animal, it would appear that the correlation between the ability to perform a certain activity and the metabolic levels is similarly with the difference between the active and the minimum metabolic levels, and not with either level nor indeed with any other standard level.

In the analogy given in figure 13, the readings are carried only to a speed of 3,500 r.p.m. Over most of this range the curve for maximum consumption was rising more rapidly than the curve for minimum consumption with the power output correspondingly increasing, but the consumption curves are beginning to draw closer together at the highest speeds. It can be imagined that if there were no structural

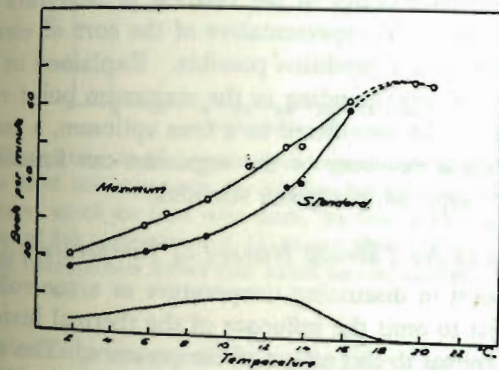


FIGURE 14.—The relation of the standard and maximum heart beat rate to temperature in alewife of the speckled trout, *Salvelinus fontinalis*. The standard rate was taken while the alewife were resting undisturbed on a bed of glass beads, the maximum immediately after they were forced to swim round in a Petri dish. The lower curve is the difference between the maximum and standard.

limitations on the speed at which the motor could be driven without flying apart, the speed could be increased until it reached a point where all the fuel the motor could consume would be needed to keep it turning over at that speed without any surplus capacity for performing any external work. When that speed was attained the power output would have returned to zero. In the example this downward trend has only just begun, but it appears that the optimum speed of rotation for power output in this particular motor was about 3,200 r.p.m.

Figure 14 shows a biological case analogous to the mechanical case illustrated in figure 13. This example was chosen particularly because the curves for maximum and minimum metabolic rates coincide at the upper end. It is otherwise perhaps a somewhat unfortunate choice since the measure taken of the metabolic rate of the organism is the activity of an organ.

The relation shown in figure 14 is that of the standard and maximal rate of heart beat to temperature in speckled trout alevins and the difference between these two levels. While the point at which the greatest difference between these two levels occurs (*ca.* 12°C.) may not be taken literally as the point at which the animal could perform the greatest amount of work in an extended period of time, owing particularly to the uncertainty of the relation of beat rate to stroke output, it may be taken as representative of the sort of circumstance which would make such a condition possible. Explained in this manner the temperature corresponding to the maximum point reached by an activity curve can be considered as a true optimum, a temperature at which the internal economy of the organism can function best to give a particular response to a given stimulus.

The Relation of the Thermal History to Temperature Optima

Up to this point in discussing temperature as a controlling factor it has seemed best to omit the influence of the thermal history on the response of the animal to this aspect of temperature. The subject has largely been ignored but some authors, notably Wells (1935b) and Mellanby (1939) have pointed out that acclimation to a given temperature level has tended to remove any initial disadvantage that that temperature level imposed on the animal when it was first encountered. Thus Wells showed that the respiratory metabolism first depressed by a low temperature rose as the animal became adapted; on the other hand the metabolic rate when stimulated by subjecting the animal to some new higher level of temperature dropped somewhat as the animal became acclimated. Mellanby showed a similar compensation with respect to the rate of the heart beat. Consequently it appears best if the optimum is to be used as a physiological index of the species, to acclimate the animals under test to each level of the factor at which it is desired to measure their activity.

Figure 15 illustrates the profound effect that the thermal history has on the optimum temperature for an activity. The activity here is the rate at which goldfish can swim steadily in water with an oxygen tension of approximately 160 mm. Hg. The level of activity elicited for these measurements was as far as could be determined,

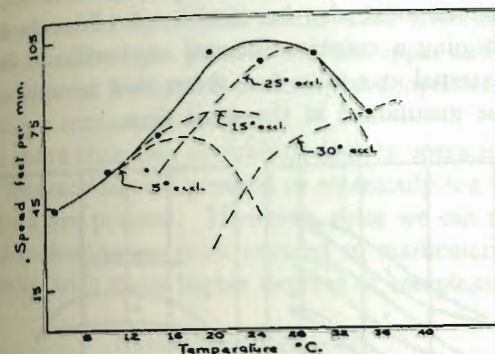


FIGURE 15.—The relation of the sustained swimming rate of goldfish to temperature. The solid line represents the relation for fish fully acclimated to each temperature at which the tests were made, the four broken lines represent the performance of fish acclimated to 5, 15, 25 and 30°C. respectively and tested over a variety of temperatures before they could become acclimated to them. From Fry and Hart (ms).

the maximum steady state, and was called forth by taking advantage of a forced movement. The heavy line shows the performance of fish presumably fully acclimated to the temperature level at which their performance was measured. The dotted lines indicate the performance of animals acclimated to a given temperature level and whose performance was measured over a series of other temperatures above and below this level.

Interaction of Controlling Factors

In the examples above no mention was made of any controlling factor other than temperature, and the optima have been termed temperature optima with no qualification. These optima could not have been pure temperature optima unless the organisms concerned were able to maintain their internal organization constant in the face of any change in all other controlling factors in the environment,

and if the experiments had been arranged to prevent the level of any potential limiting factor from approaching the limiting level.

While it is true that animals have achieved a greater independence of the other controlling factors than they have of temperature, and are more likely to be homoio-osmotic or homoio-acidic for example than they are to be homoiothermal, the influence of these other controlling factors must also be considered. Moreover, as is well known, maintaining a constant internal environment in the face of a changing external one does not mean that a constant output of activity can be maintained at the same time.

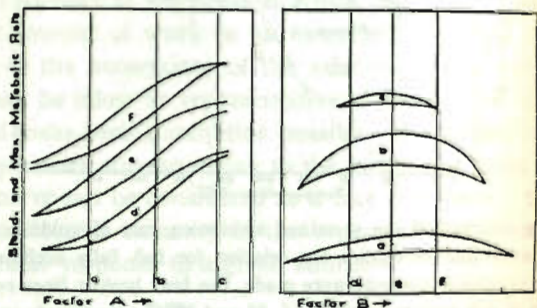


FIGURE 16.—The interaction of controlling factors; for explanation see text.

In considering the interaction of the controlling factors we can start with recognition of the fact that all aspects of the state of the medium will simultaneously influence the rates of reaction of the various substances in the metabolic chain. Thus to describe the interaction of two such factors we shall need to resort to a three dimensional graph. Since a graph of this type is rather difficult to follow unless one is able to handle the actual solid model, we shall content ourselves here by examining various two-dimensional profiles that might be taken from such a model as transverse and sagittal sections.

Let us suppose then that two controlling factors, A and B, are operating to govern the metabolic rate of a given organism. One of these factors, A, operates in a manner similar to temperature; that is the highest metabolic rate comes at a level which is very close to the incipient upper lethal level. The other factor, B, is taken

to operate more as we might imagine pH. would, that is giving a maximum that is nearer the middle of the biokinetic range for that factor.

The left panel of figure 16 shows the supposed standard and maximal metabolic rates for different levels of A at three fixed levels of B, levels d, e, and f. Each pair of lines thus represents a sagittal section through the solid figure that would result from combining the effects of A and B. The right panel shows the upper and lower metabolic levels for different levels of B at three fixed levels of A, each pair here representing a transverse section.

If there are more than two controlling factors operating in a given situation their interaction will proceed in essentially the same fashion as when only two are present. However, since we can make models in only three dimensions we must proceed to mathematics if we are to deal specifically with these higher degrees of complexity.

Concluding Remarks

It appears justifiable to conclude that with respect to the operation of temperature as a controlling factor much confusion has arisen in the literature because no clear distinction has been made between metabolism and activity, measures of activity having been considered as mere reflections of the metabolic rate. The same confusion is also apparent in the work done on the other factors of this group.

With regard to the quantitative relations between activity and temperature as a controlling factor it would appear that these can only be formulated properly and then only approximately by means of the biological formulae, which of course originate through observation of the very things they formulate. The optimum for activity would appear to be an index well worthy of all the consideration that biologists have given it and of more respect from physiologists than it has received up to the present time. It is impossible in most cases to determine the position of the optimum except by drawing a line by eye through the points relating temperature to activity, although of course Janisch (1925) fitted a catenary to certain temperature-growth curves.

When the relation of metabolism to temperature has been considered, attention has been focussed on standard metabolism, although sometimes this standard has been unwittingly the maximum

rate and has perhaps most frequently been what might be better termed routine metabolism. Describing the relation of standard (resting) metabolism to temperature is only half the story as far as the animal as a whole is concerned. The maximum rate should also be measured. The physiological group of formulae, which should properly be applied only to measures of the metabolic rate, should not be applied even to these when dealing with the intact organism or indeed to isolated systems except with great caution, since the theory

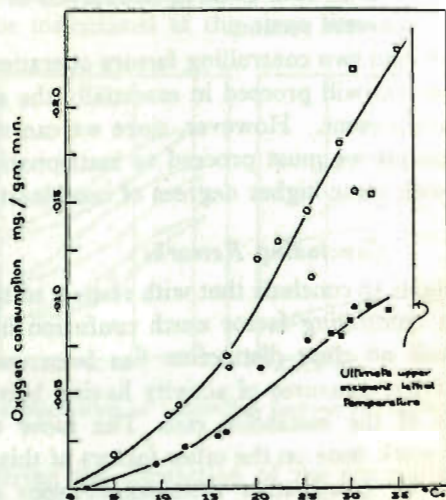


FIGURE 17.—Effect of temperature on the standard and active oxygen consumption of the bullhead, *Ameiurus nebulosus*, unpublished data of Paul and Fry. The circles and squares each indicate respectively readings taken on two individual specimens. In each case time was allowed at each temperature for thermal acclimation before the experiments were performed. Activity was induced by using a cylindrical respiration chamber mounted on a turntable.

on which they are based presumably applies strictly only to reactions between perfect gases. Again then, when dealing with metabolism as well as when dealing with activity, the best line drawn by eye through the observed points probably offers the most valuable description of the relationship.

To revert again to optima it should be pointed out that it is not at all necessary for the optimum to come well within the biokinetic

range as it does in those cases which have been cited as examples. Figure 17, which shows the relation between temperature and the maximum and standard metabolic rates in the bullhead, shows a case where the difference between these two rates increases right up to the ultimate upper incipient lethal temperature. This may be taken as evidence that the level of continuous activity would similarly increase throughout the range of thermal tolerance.

A question that has not been touched on up to this point is the relation of performance to power. Power is the ability to do work, performance is the result of the application of such work, and there need not be any simple proportionality between the two. To return to the analogy of the machine, it is well known that the speed of an automobile does not rise in direct proportion to the rate of fuel consumption; this is true even when allowance is made for the increase in no load consumption. Thus while it has been inferred that activity results from the energy released by metabolism above that needed to maintain organization and that there is a simple ratio between such metabolism and power, the level of performance which results from a given rate of work has not been specifically considered. An approximation of a relation between power and performance in the goldfish can be derived from the data presented in figures 15 and 24 since both these sets of values were derived from the same sample of fish. This relation is plotted in figure 18 which shows that the power required rises much more rapidly than does the swimming rate, a relation similar to that which holds for mechanically driven bodies.

Finally in making measurements of the operation of controlling factors on activity or metabolism, the acclimation level of the organism with respect to these levels must be described if these measurements are to have any value for physiological classification. A complete description for activity would require a three-dimensional model of which the axes would be acclimation level, level at which the activity was taking place and a measure of activity. The same is true for metabolism except that there would then also be a lower surface to the model, the two surfaces representing the two limits of metabolism. However, a simpler and probably quite adequate description can be made on two dimensions if the description is limited to the fully acclimated organism as in figures 15 and 17.

It is presumed that the remarks made concerning the operation of temperature as a controlling factor will apply equally well to the operation of other controlling factors although it is not proposed to deal with any of these specifically. It is hoped that a sufficient defence has been put forward for the removal of the controlling factors from Blackman's category of limiting factors. As has been

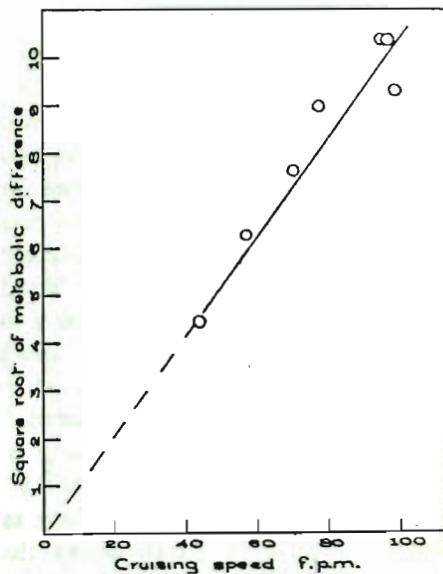


FIGURE 18.—The relation between power and performance in young goldfish. The difference between the maximum and minimum metabolic levels is taken as power, rate of cruising speed as performance. From Fry and Hart (ms.). The data from which this figure is plotted are also displayed in figures 15 and 25.

pointed out there are several fundamental differences between this group and those factors which are generally recognized as limiting factors. They differ in their seat of operation, and what is more important from the point of view of a functional classification, they also differ in the consequences to the animal which arise from changes in their levels in the environment. One of the most important of these differences from the limiting factors is that the whole complex of controlling factors acts simultaneously in a manner that is in no way related to the law of the minimum which has been so universally

associated with limiting factors. Further comparisons between controlling factors and limiting factors will be made in the following section.

LIMITING FACTORS

It hardly seems necessary to offer any preliminary description of a limiting factor beyond that already given in the introduction, so common is the term now even in the daily press. If the need of any description of the concept is felt it can be best satisfied by consulting Blackman's (1905) original paper, which is a masterpiece of exposition. Our only departure from the common usage of the term will be in restricting its meaning rather sharply. Most of these restrictions have been tacitly contained or explicitly set forth in various sections of the preceding discussion each time that some effect of the environment has been designated by some other adjective. Therefore, we shall content ourselves here with merely repeating the definition of limiting factors as it was given in the introduction.

It will be recalled that limiting factors were defined as those factors which actually enter into the chain of metabolic processes of the organism. In any governing effect that they may exert on the metabolic rate they operate by what is known as Liebig's "law of the minimum" or Blackman's "principal of limiting factors." This principle has been stated by Blackman (1905) as follows: "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the slowest factor." (page 289)

There have been two modifications made to Blackman's original concept that will not be dwelt on here. One of these relates to the sharpness of the change between the phases at which a given factor is limiting or non limiting (e.g. Burton 1936). The second modification has been the evaluation of the effect of secondary apparatus intervening between the site of the metabolism and the environment. Both of these modifications relate to the detail of operation and do not in any way question the validity of the principle that limiting factors operate by entering into the metabolic chain.

The Relation of Oxygen Supply to Oxygen Uptake

The specific example chosen for discussion of the general case of the operation of a limiting factor is the relation of the oxygen supply

to oxygen uptake. Just as the work on temperature indices deals with the quantitative effects of temperature as a controlling factor, so also does the literature dealing with the relation of oxygen supply to oxy-

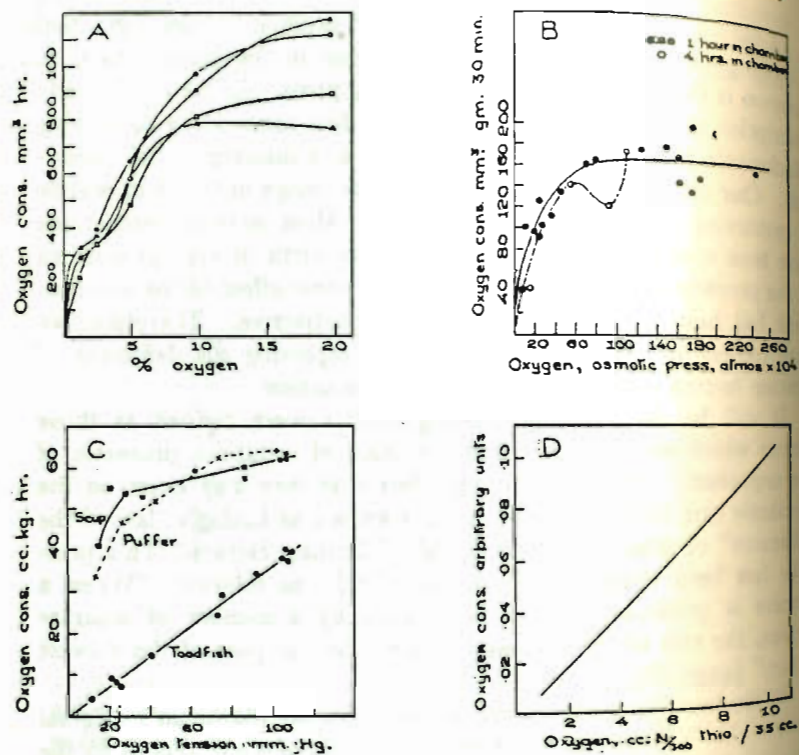


FIGURE 19.— The relation of oxygen supply to oxygen consumption in various organisms.

- A. *Dixippus morosus*, v. Buddenbrock u. v. Rohr (1923).
 B. *Fundulus heteroclitus*, Maloeuf (1937).
 C. Various marine fish, Hall (1929).
 D. *Homarus americanus*, Amberson, Mayerson and Scott (1924).
 Figures A, B and C reprinted with permission.

gen uptake deal with the effects of oxygen as a limiting factor. For the details concerning this work the reader is referred to the comprehensive reviews of v. Ledebur (1939) Maloeuf (1937), and Tang (1933). Figure 19 gives a number of representative curves showing the

Two important contributions on the relation between Oxygen consumption, Oxygen requirements and Oxygen pressure in fish were overlooked when the section on limiting factors was written.

These are:

- Lindroth, A. 1940
 Sauerstoffverbrauch der Fische bei verschiedenem Sauerstoffdruck und verschiedenem Sauerstoffbedarf. (Zeitschrift für vergleichende Physiologie) 28: 142-152.
- Lindroth, A. 1942.
 Sauerstoffverbrauch der Fische II. Verschiedene Entwicklungs- und Altersstadien vom Lachs und Hecht. (Zeitschrift für vergleichende Physiologie) 29: 583-594.

In these, Lindroth expresses essentially the same point of view with regard to Oxygen as a limiting factor as has been given here with respect to the level of no excess activity. He establishes some levels of no excess activity for Salmo salar, Leuciscus rutilus and Esox lucius.

relationship of oxygen uptake to oxygen supply as it has been determined experimentally. Briefly it may be stated that the relation has generally been found either to be linear over the range of oxygen values where the rate is affected by the level of the oxygen supply, or to be hyperbolic. The linear relations bear out Blackman's original assumption, the hyperbolic curves are more consistent with more recent theories of diffusion (Tang 1933).

The term "respiratory dependence" has been employed to describe the phenomenon of the respiratory rate being related to the oxygen supply. The respiration rate becomes independent of the oxygen supply above a certain critical value.

One important feature of the phenomenon of respiratory dependence, the significance of which appears to have been universally overlooked, except possibly by v. Ledebur (1939), is the fact that respiratory dependence is generally well expressed, at least in the more highly organized animals, over a wide range of levels of oxygen supply only when the animals are respiring at their maximum rate. This phenomenon has however, been often unconsciously employed in the experimental technique. Thus Maloeuf (1937) in his experiments, made measurements only during the first hour that fish were in the respiration chamber. The results found by Black, Fry and Scott (1939) make it extremely probable that the fish would still be respiring at a rate approaching their maximum during that period, presumably as a result of the handling they receive while being introduced into the chamber. When the respiratory rate is measured in the Warburg apparatus the continual motion serves to keep the animal stimulated. Thus it may be said that whereas in the case of literature dealing with temperature as a controlling factor activity and metabolism have been confused, in the literature dealing with oxygen as a limiting factor activity has been ignored.

Consideration of the fact that the greatest respiratory dependence has been found using animals respiring at their maximum rate will bring us to the essential difference between the operation of a limiting factor and that of a controlling factor, not, it is true through logic, but by the association of ideas. A controlling factor it will be recalled, is one which governs both the maximum and minimum rates of metabolism. A limiting factor, on the other hand, exerts its control only on the maximum rate of metabolism, for once the limiting factor

has attained a level which reduces the metabolic rate to the minimum required to maintain the vital processes of the animal, that factor has reached its incipient lethal level. At levels beyond this the animal must go steadily into some metabolic deficit which will accumulate until death ensues.

We can make use of this attribute of limiting factors to derive what, if obtained with proper experimental precautions, would seem to be a very valuable index of animal activity. This index might be designated *the level of no excess activity* or perhaps *the level of standard activity*. It can be derived as follows.

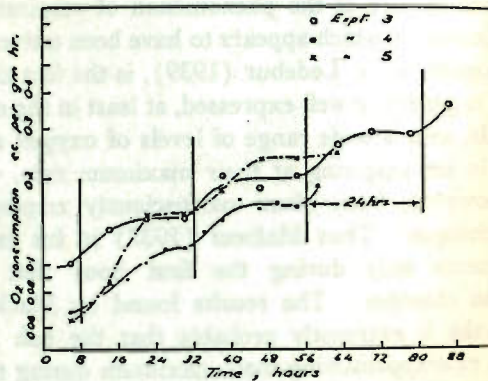


FIGURE 20.—A persistent cycle of activity influencing the metabolic rate. From data in table 2 Wells (1935a). These data illustrate a 24 hour cycle of activity superimposed upon the effect of raising the temperature by equal steps at constant intervals.

The first step is to measure the standard level of metabolism of the organism, taking care that it is receiving somewhere in the neighbourhood of the minimum of external stimuli, and that it is at the bottom of any persisting cycle of activity such as Clausen (1936), Gompel (1937), and Spencer (1939) have demonstrated. Such cycles of activity can wreck what are otherwise the most careful of experiments. An example of such a cycle in fish is given in figure 20 which shows a persistent 24 hour cycle of activity superimposed on the effect of changing temperature which was the effect that the author desired to measure. Care should also be taken to ensure that

no other factor might be near its limiting level. The controlling factors should be kept constant.

After the standard level of metabolism has been determined the animal is then stimulated to elicit its maximum continuous level of work, and during this process its metabolism is measured over a series of levels of the factor in question, until in spite of continued stimulation the metabolic rate drops to a level representing the standard

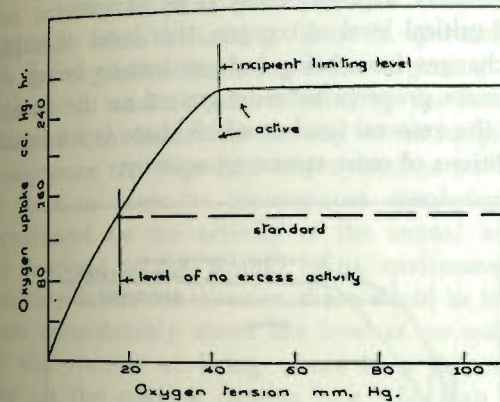


FIGURE 21.—The level of no excess activity for oxygen for young goldfish acclimated at 25°C. as determined from measurement of standard and active rates of oxygen uptake. From Fry and Hart (ms.).

metabolic rate or below. An example of this determination is given in figure 21 which shows the data from which the oxygen tension of no excess activity for the goldfish at 25°C. can be derived.

It is extremely interesting to note that Henderson (1939) gave such a level of no excess activity as the reason that man had never been able to climb the last thousand feet of Mount Everest. He argued that since the resting metabolism of man requires an oxygen consumption of 250-350 cc. N.T.P./min., an amount which could be supplied at 29,000 feet only by the maximal respiratory effort even when fully acclimated to low oxygen, it would not be possible for anyone to carry on the activity necessary to finish the climb, unless supplied with an artificial source of oxygen.

The level of no excess activity cannot of course be an index of absolute magnitude, and is actually open to more objections than

obtain for the standard metabolic rate. For instance, in measuring the maximum rate of oxygen uptake the accessory respiratory mechanism is working to its utmost, and the cost of respiration may be many times greater than it would be under the standard conditions. However, such a fault might be allowed since it tends to compensate for the fact that the standard rate is above the minimum. Van Darr (1938) gives a fine example of the increasing cost of respiration in the trout, *Salmo shasta*, at lower tensions of oxygen.

The so-called critical level of oxygen, that level of supply where the respiration changes from being independent to being dependent, perhaps should more properly be redesignated as the *incipient limiting level* that is the external level at which there is no limiting effect even under conditions of most strenuous activity.

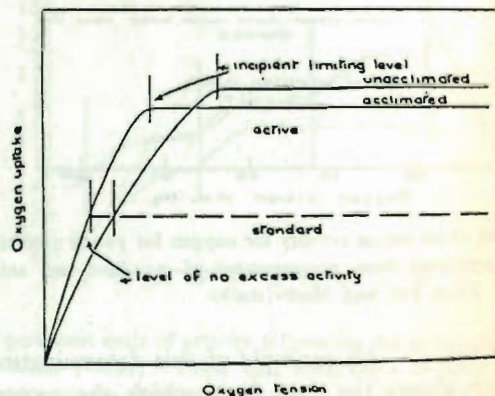


FIGURE 22.—A possible effect of acclimation on the level of no excess activity.

Acclimation to Limiting Factors

Up to this point we have not considered in our discussion of limiting factors the relation of the history of the organism to the effect the factor concerned has upon it. Nor shall we consider it, except to speculate, for although much is known of the physiology of acclimation to low levels of oxygen, especially in man, its relation to activity does not appear to have been yet set forth in general terms.

It may probably be safely assumed that the effect of acclimation to low environmental levels of oxygen will be to reduce the level of no excess activity. Perhaps it may also be safe to assume that the

minimum metabolic level will remain constant. If such were the case the effect of acclimation might be represented graphically as in figure 22. In any event the hypothesis is amenable to direct test.

Discussion of acclimation presupposes that some stress is exerted on the organism which is the stimulus that brings out the adaptive response. The manner in which the environmental stress is imposed by a limiting factor appears to be different from that which occurs when activity is being governed by a controlling factor. It may be said that when a limiting factor is operating the stress is imposed by the organism itself, for if the organism remained completely quiescent it would not be affected by the factor in question, unless of course that factor were nearly at an incipient lethal level and in consequence the organism might need to put forth considerable effort just to meet its maintenance metabolism. The stress then is occasioned by the activity of the animal arising from its attempts to respond to the stimuli of its environment. If oxygen were the limiting factor for instance, there would be levels of oxygen, perhaps even considerably above the level of no excess activity, at which just the routine of living would keep the organism almost continuously on the edge of oxygen lack. In such a manner presumably is the environmental stress exerted which elicits the adaptive response.

It can be seen that the corollary to the proposition in the preceding section is that the effect of a limiting factor is to limit to a certain level the overall activity of the organism, although it may still be capable of putting the same energy into short bursts of activity as before. The lower the level of the limiting factor, the greater the difficulty of repaying any metabolic deficit that may be incurred in even short bursts of activity. The remarks of Henderson (1939) referred to above show the situation clearly.

Interaction of Limiting and Controlling Factors

We are now in a position to consider further the conditioned optimum. Previously we considered the interaction of two or more controlling factors, now we can add to this a discussion of the interaction of a controlling factor or combination of controlling factors with a limiting factor, or indeed, combination of limiting factors. We

shall illustrate this discussion by considering the interaction between oxygen as a limiting factor and temperature as a controlling factor.

Before we can work out this interaction it is necessary to examine the effect of temperature on respiratory dependence. One such effect has already been shown in figure 2, which shows the relation of temperature and oxygen tension to the cutaneous respiration rate in the

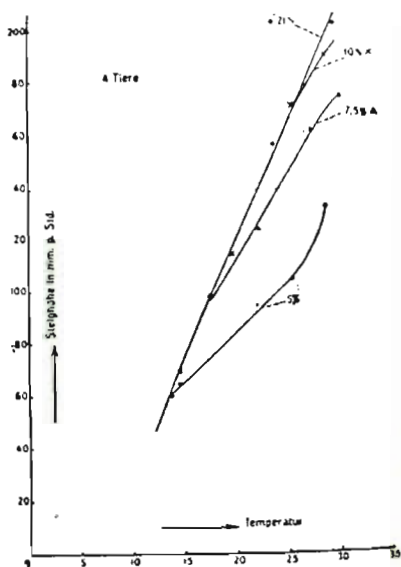


FIGURE 23.—The relation between respiration rate, oxygen tension and temperature in the stick insect *Dixippus morosus*. From v. Buddenbrock & Rohr, 1923.

frog. In figure 2 (page 10) it will be seen that when the respiration rate has reached a particular level that rate cannot be exceeded when the oxygen tension is restricted to a level which just supplies that need, although the temperature may be increased, as was pointed out on page 9. Another relation between respiration rate, oxygen tension and temperature, which can be expected to occur more commonly in the metazoa is shown in figure 23. Here there is no series of plateaux as figure 2 presents; instead of a constant level for the rate of oxygen uptake continuing with increasing temperature when a limiting level of oxygen tension is reached, there is a gradual rise with increasing temperature but this

rise is related to the oxygen tension. The explanation of the difference in the response to increasing temperature shown in the two figures lies in the fact that in the cutaneous respiration of the frog there is no accessory respiratory apparatus involved, whereas there is in the case of *Dixippus*. When accessory respiratory apparatus is involved, oxygen tension is no longer a measure which is equivalent

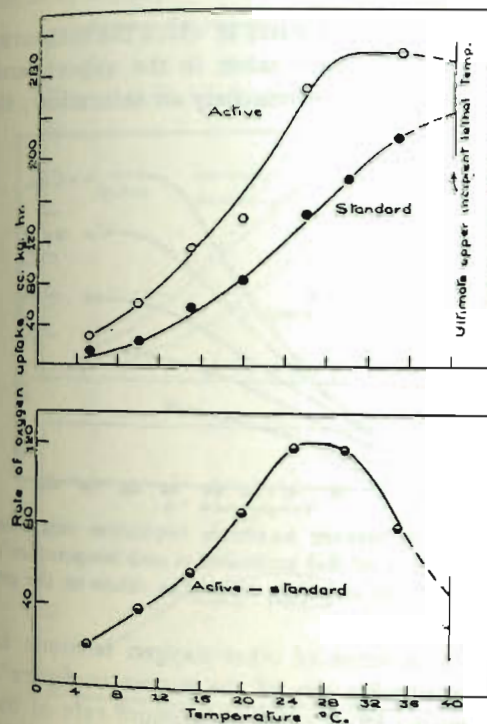


FIGURE 24.—The relation between temperature and metabolism in young goldfish acclimated to each temperature before the measurements were taken. From Fry and Hart (ms.).

to oxygen supply, since increasing temperature stimulates the operation of the ventilatory apparatus, or whatever the accessory apparatus may be, and thus presents a greater supply of oxygen to the respiratory surfaces for a given amount in the medium. Pütter it may be presumed chose his experimental material carefully to exclude this complication. We can now turn to the specific case chosen to illustrate the interaction between limiting factors and controlling factors.

Figure 24 shows the relation between temperature and the maximum and standard rates of metabolism in the goldfish. Previously (page 32) it was pointed out how such data as are presented in figure 24 possibly form the rational basis for an interpretation of optimal temperatures for activities. The same principle will be extended here to the production of a similar optimum conditioned by the tension of available oxygen.

The oxygen tension of the water at which the measurements of the maximum rate of uptake were taken in the experiments providing the data for figure 24 was approximately air saturation; the maximum

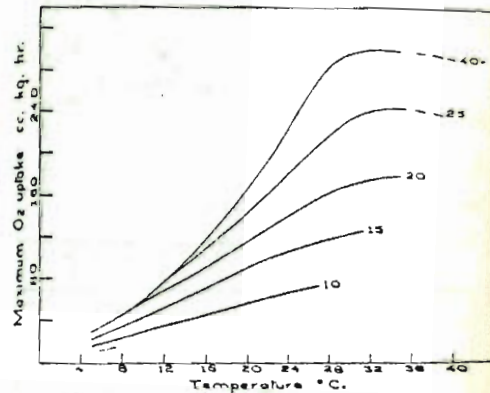


FIGURE 25.—The relation between maximum respiration rate, temperature, and oxygen tension in young goldfish acclimated to each temperature before measurements were taken. (Fry and Hart, ms.) The values on the graph are oxygen tensions in mm. Hg.

rates of uptake at a series of other oxygen tensions are shown in figure 25. By combining any of the curves in figure 25 in which oxygen has a limiting effect on the maximum rate of oxygen uptake with the curve depicting the minimum oxygen requirement, that is the oxygen required to maintain the standard metabolic rate (figure 24) a particular case of the interaction of a controlling factor and a limiting factor will be obtained. Such a case is illustrated in figure 26.

Two features are apparent in figure 26. Reducing the oxygen tension to 25 mm. Hg. reduces progressively the degree of activity possible at the higher temperatures, as indicated by the increasing proximity of the standard and maximum metabolic curves. Also, at a certain temperature, the maximum activity is reduced to the level of the standard requirements, and not only the activity but the existence

of the animal is terminated at temperatures just beyond this point, death being due to oxygen lack.

The lower curve in figure 26 is derived as in figure 13 by plotting the difference between the maximum and standard levels of metabolism against temperature. The temperature at which this point reaches its highest value is a temperature optimum conditioned by the limiting effect of 25 mm. of oxygen.

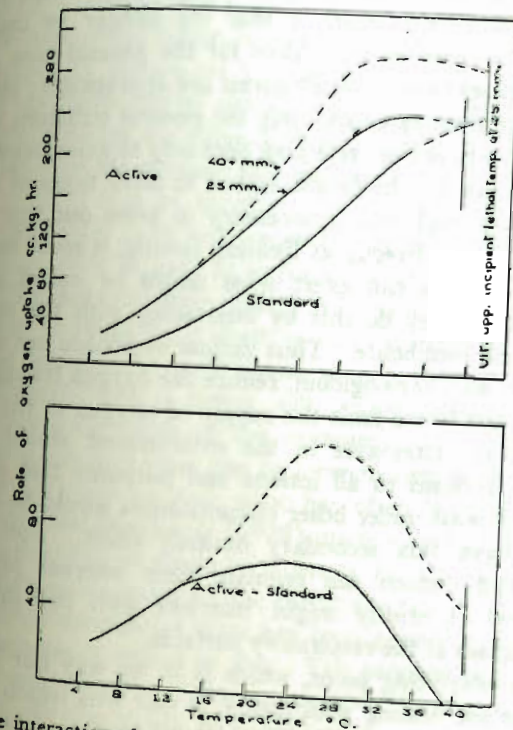


FIGURE 26.—The interaction of a limiting and a controlling factor. For explanation see text. Data from figures 24 and 25.

The inclusion of another limiting factor in the scheme would only clip off more of the maximum metabolism over some part of the temperature range, with a resulting effect on the position of the conditioned optimum or on the extent of the biokinetic range. It may be said that limiting factors operate consecutively, as indeed has been held since the publication of Blackman's (1905) paper, while as has been pointed out earlier, controlling factors act concurrently. Two homely similes, which give point to the difference, are that

limiting factors are like a chain, which is no stronger than its weakest link, while the controlling factors are like a rope, which is as strong as the sum of its threads.

Concluding Remarks

It is hoped that this exposition of the operation of oxygen as a limiting factor illustrates the principles in a manner sufficiently comprehensive to allow the subject to be closed with little further discussion, although it is realized that the danger in using specific examples is that they may be taken for the general case. Examples refer only to cases to which their terms are appropriate; terms may be different in different cases and only the general structure is the same. For instance we have been referring here only to oxidative metabolism; the principles but not the details extend to other types of metabolism.

A final paragraph seems necessary to point out that while only metabolites can act directly as limiting factors, it must be recognized that non-metabolites can exert what might be called a secondary limiting effect. They do this by interfering with the normal interchange of some metabolite. Thus carbon monoxide can for example, by combining with haemoglobin, reduce the oxygen transport capacity of the blood and hence limit the supply of oxygen to the tissues. In this way carbon monoxide in the environment would produce an effect on metabolism to all intents and purposes that of a limiting factor. Even what under other circumstances would be a controlling factor can have this secondary limiting effect. For instance in aquatic animals which can regulate their internal pH, a certain external level of acidity might interfere with the interchange of respiratory gases at the respiratory surfaces.

Another interesting point, which is in no way our concern here since we are not dealing with plants, is that ions which are involved in photosynthesis may perhaps on occasion operate simultaneously as controlling and limiting factors. Thus the rate of photosynthesis may be limited by the rate of supply of a particular ion while also the contribution that that ion makes to the ionic complex of the cell medium may influence the metabolic rate of the cell.

ACCESSORY FACTORS

While a separate category has been erected for accessory factors and they are defined as those factors that impose upon the organism a metabolic load in excess of that to which the organism is restricted

by whatever factor is governing its maximum metabolic rate, this category is one of convenience rather than of fact. It is merely a useful heading under which to bring together various interactions of the last three categories which result in the death of the animal. This was made plain in the preceding section where discussion of the interaction of controlling and limiting factors was ended at the point where the limiting factor had reduced the maximum uptake to the minimum need. Beyond this point it is proposed that we speak no longer of the controlling factor, but call it an accessory factor instead.

When accessory factors are operating, the lethal effects attributable to their operation can be appraised in terms of the interaction of the factors involved but the value of this possibility for analysis lies at present far more in the promise than in the fulfilment.

At this point it will be necessary to introduce another premise which will presumably meet with general acceptance. If the operation of an accessory factor is such as to force the animal to accumulate a metabolic deficit that ultimately results in its death, the amount of that deficit required to bring about death is either a constant, independent of the rate at which it is accumulated, or is a function of that rate. The rate at which such a deficit will accumulate will be a function of the metabolic needs of the organism and of the difference between these needs and what can be interchanged with the environment. These propositions state what has often been inferred. For instance Sumner and Doudoroff (1938) made use of the rate of dying of *Gillichthys mirabilis* in dilute solutions of KCN in sea water or in boiled sea water as an index of the metabolic rate. This of course is but an isolated example of what has been general practice, chosen particularly because it relates to fish. The propositions can then be taken as well established in biological practice if not in fact. Let us now see what help they might be in analysing certain lethal effects of the environment.

In the first place it may be stated that when lethal effects are brought about by the operation of accessory factors, the rate of dying is influenced by the metabolic rate of the organism. This of course is common knowledge and the example to follow is inserted to carry the thread of the argument rather than to introduce the subject. The operation of an accessory factor as opposed to what appears more likely to be a pure lethal effect can be illustrated by contrasting the difference in the progress of the lethal effect of high temperature with

that of low oxygen, both lethal effects being considered with respect to fish.

The rate of dying of fish in high temperatures has been demonstrated on a number of occasions (e.g. Fry, Hart and Walker 1946) to be independent of their size. In others where a correlation between order of death and size has been observed, this correlation has been inverse, the larger fish being the more sensitive. (Huntsman and Sparks 1924). It is well known that the metabolic rate per unit weight of organisms of the same species tends to be an inverse function of their size. A well worked-out example of this phenomenon in fish has been given by Wells (1935b). Clearly then in a great many cases there is no correlation between the metabolic rate of fish and the order of sensitivity to lethal levels of high temperature.

On the other hand the rate of death of members of one species of fish exposed to oxygen-free water is very definitely related to their metabolic rate as inferred from their size (Wells 1913).

This appears to be the appropriate place to interpolate a few remarks concerning experimental procedure in measuring a lethal effect when an accessory factor is concerned. When measuring the lethal effect of oxygen lack for instance, precautions must be taken to ensure that the metabolism of the organism remains in some standard condition throughout the experiment. The validity of such a measurement depends upon this precaution as much as does that of any measure of metabolism itself.

In our postulates we have ascribed the rate of dying occasioned by accessory factors to two circumstances, the metabolic rate and the level to which some product which is the consequence of the metabolic deficit must rise in order to be lethal. If we could separate these two influences we could make interesting comparisons between species, for we could then in effect eliminate the influence of the metabolic rate. It is possible that in the case of fish such a separation could be achieved by arranging apparatus so that the metabolic rate could be measured immediately before introducing oxygen-free water.

We could continue to speculate in this vein for a considerable further period. However, enticing as these speculations may be, we are building a theoretical house of cards and would be well advised to cement the lower storey with a little experimental sealing wax before proceeding to erect the structure higher.

In considering accessory factors we have spent most time discussing the case where the maximum rate has been reduced below the minimum requirement. This is not the only way in which the incompatibility between need and satisfaction can arise, nor is it the only one which has been mentioned, but the other case was taken up in the introduction and may well have slipped from mind. The case given there, that of the death of fish due to their inability to maintain their osmotic balance at low but not otherwise lethal temperatures was one in which the minimum requirement was raised above the maximum metabolic rate.

Finally it should be pointed out that there are cases in which the rate of death due to the operation of an accessory factor may appear to be independent of the metabolic rate due to extraneous circumstances. Thus while fish exposed to boiled water die in order of size, there is no such correlation at all between size and order of death if death is brought about by simply removing them from the water and exposing them to air. A small fish may live as long under these circumstances as does a large one of the same species. (Poli-manti, 1914, Tchang-Si and Yung-pin Liu, 1946). While in both cases death is due to anoxia, this anoxia is brought about by different means. When fish are exposed to boiled water anoxia is due to lack of oxygen in the medium, but when they are exposed to air they fail to take up a sufficient supply of oxygen, not because of a lack of supply of that element but because the mechanical unsuitability of the medium prevents the gills from functioning. Therefore when fish with no specialized apparatus for terrestrial respiration are exposed to air they are not entirely deprived of oxygen because some can still be absorbed through the skin, and the relatively greater body surface of the smaller fish tends to compensate for their relatively greater metabolic rate. Indeed the whole situation is an interesting demonstration of the well-known law relating metabolic rate to surface area.

RECAPITULATION

While the order of treatment of the various categories of the environmental factors followed above appears to be logical from the point of view of developing a sequence of thought on the subject, the material can now be arrayed in what may be a better order for the purpose of displaying the interrelation between the various factors and the organism. This rearrangement is introduced in figure 27.

The four panels in figure 27 should be considered in order from the top left to the bottom right.

The top left panel presents a generalized picture of the relation between the maximum and minimum levels of metabolism, and of the

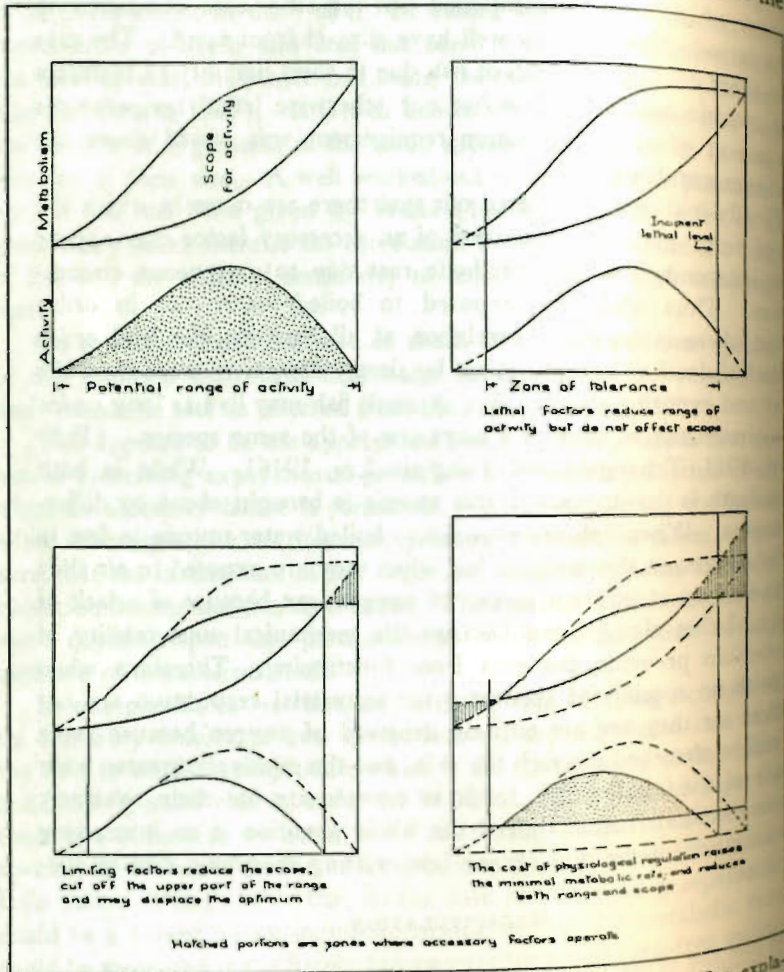


FIGURE 27.—The interaction of the environment and the organism. For explanation see text.

scope for activity in relation to the controlling factors. The picture presented here is one which is rarely or perhaps never attained for

it is one in which the organism is allowed its complete expression insofar as its response to the controlling factors is concerned. At the one end of the range the minimum metabolic rate is zero, and hence the maximum rate is zero also. At the other end of the range the minimum rate absorbs the total metabolic capacity of the organism and thus again coincides with the maximum metabolic rate. This coincidence at the upper end of the range, it must be emphasized, is not to be thought of in this instance as being occasioned by the operation of any limiting factor. The distance between these two points of coincidence of the maximum and minimum rates represents the potential range of the controlling factors over which the organism might be active if nothing else intervened. This range might be termed the *potential range of activity*. The distance between the maximum and minimum metabolic rates of metabolism at any point within this range of the controlling factors might be termed the *scope for activity*. This basic description of the capacities of the organism has been made perforce with reference to the controlling factors for these factors enter inevitably into any situation. Let us again now see how the other factors modify this basic picture.

The upper right panel shows the manner in which the identity which is acting as the controlling factor may operate as a lethal factor to reduce the possible field of existence and activity. The lethal factor has been depicted as slashing off both the upper and the lower end of the potential range of activity. Two examples of such an abrupt termination to activity at the upper end of a range of a controlling factor have been given in the text. These are the relation of the incipient upper lethal temperature to the maximum and standard rates of metabolism in the bullhead (figure 17) and that between the lethal and the response to a stimulus in the speckled trout (figure 12). No specific case has been cited of a similar lethal effect at the lower end of the range but it can be well imagined that such an effect obtains in an animal like the speckled trout which is quite active at 0°C. but which must surely perish at a temperature a degree or two below that point. It is considered that the lethal factors have no effect on the scope for activity within the biokinetic range, nor do they influence the absolute position of the optimum, although they may affect its relative position in the biokinetic range or even obliterate it entirely if the upper incipient lethal is reached at a low enough level with re-

spect to the potential range for activity, as is apparently the case in the bullhead (figure 17).

The abrupt termination of the biokinetic range without affecting activity may well be questioned. As the case has been stated here there has been no room left for the well-known time factor (Blackman 1905). This has been so because the lethal limit chosen is the incipient lethal level and presumably it will be beyond this level that the time factor will be well expressed. It is difficult to say exactly how justifiable it is to take the stand that there is no progressive reduction of the maximum rate of metabolism towards the upper end of the zone of tolerance before the zone of resistance is reached, and the matter requires careful investigation using material for which the lethal limits have been determined with some precision. Such experiments as those of Pantin (1923) on *Amoeba* in which his subjects moved more slowly at a given temperature when returned to it after a period at a higher one are not necessarily evidence of anything but thermal acclimation. If the incipient lethal level is also taken as the lower limit of the biokinetic range, there may perhaps be species in which there is no biological zero. Perhaps however this interesting heresy should not be pursued too far at the present.

The lower left hand panel adds the effect of a limiting factor on activity within the zone of tolerance delimited on the upper right panel. The effect of the limiting factor is to reduce the scope for activity and to displace the optimum to the left. The level of the limiting factor has been so chosen that the lethal effect in the zone of resistance is always brought about by the combination of an accessory factor with the lethal factor.

If we disregard the lethal factor it may be noted that the reduction of the biokinetic range by a limiting factor comes at the upper end of the range of the controlling factor in the diagram given. The general case would be that the range would be cut at whatever point the minimum metabolic needs were the highest. In such a case as was imagined in the right panel of figure 16, the biokinetic range would be reduced by having a gap in the middle. Or if the limiting effect were not quite so severe, there might be two maxima of activity separated by a central depression. It is possible that this is the explanation for the bimaximal curves for growth rate of *Colpidium striatum* in relation to pH found by Elliott (1933).

In the final panel of figure 27 the effect of the need for further physiological regulation in the face of both the limiting factor and the lethal factor is illustrated. The metabolic requirement for carrying out this further physiological regulation has been added to the minimum metabolic rate. This raises the baseline and reduces the scope for activity. Also in the correct combination of circumstances it can still further reduce the biokinetic range at either end, death beyond this point being due either to accessory factors or to a mixture of accessory and lethal factors.

Sometimes physiological regulation may be obtained as a by-product of metabolism used for activity, as is the case when heat produced by the muscles in performing work is used to maintain the body temperature above that of the environment. Such regulation as this presumably does not subtract from the scope for activity. In all other cases, although the cost may not be great it presumably must enter into the question.

Concluding Remarks

The immediate objective in erecting this classification of environmental factors was to provide a basis for a description of animals based on measurements of their activities as influenced by the various identities in the environmental complex. The problem with which we are faced in the physiological description of organisms in relation to the environment is that of assessing reality by means of restricted and artificial standards: for there is no profit in the classification unless a sample of the animal's functioning can be taken as representative of the whole, nor is there any control over the conditions without some artificial manipulation. It is hoped that this paper will be a contribution towards the attenuation of the fundamental difficulty inherent in all experimental work, that is the difficulty of knowing the precise meaning of a specific experimental result in relation to the general case. With a classification of the environment in relation to its effects on metabolism, and with some statement of the relation between metabolism and activity, some logical portioning of effort is possible. And even if the classification and the statement may prove to be erroneous they are not valueless, for there is a great deal more value in having things corrected than there is in never stating them; the road to truth lies much through argument.

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