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Rate of Metabolism
and
Food Requirements of Fishes

by

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RATE OF METABOLISM AND FOOD REQUIREMENTS OF FISHES

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Editors' Foreword

This translation of Professor G. G. Winberg's monograph is reproduced with the author's kind permission. It represents a cooperative enterprise of the Fisheries Research Board of Canada, the Department of Zoology, University of Toronto, and the Ontario Department of Lands and Forests, Research Division.

Two preliminary English versions were used: one prepared by Mrs. E. Jermolaev on behalf of the Ontario Department of Lands and Forests, the other by the Bureau for Translations, Foreign Language Division, Department of the Secretary of State of Canada. These were compared and brought into agreement; then both of the editors and Mrs. Jermolaev once more checked the revised version, particularly as regards the technical terminology, returning frequently to the original text in order to clarify difficult passages.

Some more or less arbitrary decisions were made concerning what word equivalents to use, and there is also some special terminology. The more important of these are listed below:

adaptatsii͡a	1. acclimation (physiological response of an individual to any change in environmental conditions); 2. adaptation (an hereditary characteristic of a species which favours its survival in a given locality or habitat--cf. page 38 of the translation).
akklimatizatsii͡a	1. acclimation; 2. acclimatization (the establishment of a species in a new geographical region). N.B. The English word acclimatization is sometimes used with the meaning given for acclimation above, but this has been avoided in this translation.
akklimatizirovat'	1. to acclimate; 2. to acclimatize
dykhanie	respiration
gazoobmen	respiration, respiratory exchange
intensivnost'	rate, (less often) intensity
kal	calorie, gram-calorie
kkal	Calorie, kilogram-calorie
ob'ekt	1. subject, specimen; 2. (less often) species

obmen, or obmen veshchestv	metabolism (see page 18 of the translation for the various kinds of metabolism)
uroven' obmena	level of metabolism, metabolic level (see page 93 of the translation)
skorost' obmena, intensivnost' obmena	metabolic rate
potreblenie kisloroda	oxygen consumption
prirost	growth, increase, gain (in weight, rather than length)
prisposoblenie	= adaptatsii͡a (both meanings)
respiratsionnai͡a kamera respiratsionnai͡a skli͡anka respiratsionnyĭ sosud respirometer	respirometer respiration chamber respiration vessel
spetsificheskiĭ	specific
sreda	environment; medium
temperatur sredy	ambient temperature
vid	1. species; 2. (less often) form
vidovoĭ	species (adjective)

A list is given below of the fishes mentioned only by their Russian names in the Russian text. Corresponding scientific names and English names are given, where possible. In the translation, English names are used as far as possible, otherwise the Russian name.

American char (amerikanskai͡a palii͡a)	*Salvelinus fontinalis*
Atlantic salmon (losos', sëmga)	*Salmo salar*
Baikal omul (Baĭkal'skiĭ omul')	*Coregonus autumnalis*
Baikal sculpins (bychki)	*Cottus* and allied genera
beluga	*Huso huso*
bream (leshch)	*Abramis brama*
brook lamprey (ruch'evai͡a minoga)	*Lampetra planeri*
brook trout (forel' ruch'evai͡a)	*Salmo trutta* ("morpha" *fario*)
burbot (nalim)	*Lota lota*
chub (golavl')	*Leuciscus cephalus*
chum salmon (keta)	*Oncorhynchus keta*

crucian carp (karas)	*Carassius carassius*
cyprinodonts (karpozubye)	Cyprinodontidae
dace (elets)	*Leuciscus leuciscus*
eel (ugor')	*Anguilla anguilla*
goldfish (zolotai͡a rybka)	*Carassius auratus*
gudgeon (peskar')	*Cottus gobio* (or *Gobio gobio*)
herring (sel'd')	*Clupea harengus*, *C. pallasi*
ide (yaz')	*Leuciscus idus*
inconnu (belorybitsa)	*Stenodus l. leucichthys*
inconnu (nel'ma)	*Stenodus leucichthys nelma*
Ladoga whitefish (sig ladozhskiĭ)	*Coregonus lavaretus baeri*
lamprey (minoga)	*Petromyzon* or *Lampetra*
largemouth bass (chërnyĭ okun')	*Micropterus salmoides*
loach (v'i͡un)	*Misgurnus fossilis*
lungfish (dvoi͡akodyshashchai͡a)	*Protopterus aethiopicus*
minnow (gol'i͡an)	*Phoxinus phoxinus*
mirror carp (zerkal'nyĭ karp)	*Cyprinus carpio*
muksun (a whitefish)	*Coregonus muksun*
Neva smelt (nevskai͡a kori͡ushka)	*Osmerus mordax*
ninespine stickleback (deviatiiglai͡a koli͡ushka)	*Pungitius pungitius*
osëtr (a sturgeon)	*Acipenser güldenstädti*
peli͡ad (a whitefish)	*Coregonus peled*
perch (okun')	*Perca fluviatilus*
pike (shchuka)	*Esox lucius*
pipefish (morskai͡a igla)	*Syngnathus* or *Nerophis*
pond carp (karp)	*Cyprinus carpio*
rainbow trout (forel' raduzhnai͡a)	*Salmo gairdneri*
ripus (a form of cisco)	*Coregonus albula ladogensis*
river lamprey (ruch'evai͡a minoga)	*Lampetra fluviatilus*
roach (plotva)	*Leuciscus rutilus*
rudd (krasnopërka)	*Scardinius erythrophthalmus*
ruffe (ërsh)	*Acerina cernua*
scaled carp (cheshuĭchatyĭ karp)	*Cyprinus carpio*
seahorse (morskoĭ konëk)	*Hippocampus* sp.
scorpionfish (morskoĭ ërsh)	*Scorpaena* sp.
sculpin (podkamenshchik)	*Cottus gobio*
sevri͡uga (a sturgeon)	*Acipenser stellatus*
sheatfish (som)	*Silurus glanis*
ship (a sturgeon)	*Acipenser nudiventris*
smelt (kori͡ushka)	*Osmerus mordax*, *O. dentex*
spiny loach (shchipovka)	*Cobitis taenia*
sterlet (sterli͡ad)	*Acipenser ruthenus*
sticklebacks (koli͡ushki)	Gasterosteidae
stone loach (gólets)	*Nemachilus barbatulus*
sturgeons (osetrovye)	*Acipenser* and *Huso*
tench (lin')	*Tinca tinca*
trout (forel')	*Salmo trutta* ("morpha" *fario*)

Ural ripus	*Coregonus albula* spp.
vobla (a form of roach)	*Leuciscus rutilus caspicus*
whitefish (sig)	*Coregonus lavaretus*
whitefishes (sigovye)	*Coregonus* spp.
wild carp (sazan)	*Cyprinus carpio*
zander (sudak)	*Stizostedion* (or *Lucioperca*) *lucioperca*

The technical conventions used are as in other translations reproduced by the Fisheries Research Board. In particular, materials put in square brackets always consist of notes made by the editors or translators, or else are Russian words included for the purpose of identifying the author's meaning when there might be ambiguity. Also, page numbers of the Russian original are inserted in the English text in square brackets. *The page references throughout the text are to this original pagination*.

In conformity with English usage, the initials of individuals named in the text have often been omitted. All temperatures given are in degrees Centigrade.

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Editors

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CORRECTIONS

(Page references are to the pagination of the translation)

Page 1, paragraph 2, line 3: instead of "if", read "is".

Page 34, paragraph 1, line 20: delete "rate".

Page 132, paragraph 2, line 2: instead of "testing", read "treating".

Page 133, footnote: delete the comma at the end of line 1.

Page 179, paragraph 2, line 2: instead of "is", read "are".

Page 191, Chertov, line 2: instead of "black-spined", read "black-backed".

Page 202, Wolsky and Holmes, line 1: instead of "in", read "and".

Chapter I. [page 3]

Problems and Methods in the Study of Fish Metabolism

1. General problems in the study of the metabolic rate of fish

Fish metabolism is being actively studied both because of its great importance in comparative physiology, and because of its importance to the practice of fishery management.

It is necessary to know the physiological peculiarities of fish well in order to develop a scientific basis for fish culture and management. Metabolic rate if of major importance because, in one way or another, it affects the speed of all vital processes. Metabolic rate reflects the expenditure of energy of fish, and consequently their food requirements. Metabolic rate is linked directly with oxygen requirements, and these must be understood in order to solve many problems associated with rearing fish, holding fish, shipping live fish, etc.

All this has been realized by Soviet scientists, who in recent years have published many works containing valuable information that describes fish metabolism quantitatively. However, the material on the metabolic rate of fish that has accumulated in the Soviet and foreign literature, done by different methods and from different points of view, has not yet been critically examined and summarized. Therefore, in spite of the abundance of published material it is still not possible to answer such a simple question as: "What is the metabolic rate of a fish?" We refer, of course, not to particular measurements made under experimental conditions, but values which describe the metabolic rate of fish in nature.

This is not at all a new approach to the question. On the contrary, the very first attempts at a quantitative study of the respiration of fish [page 4], made more than a hundred years ago, were done for this purpose (Humbolt and Provençal, 1811). As the results of the study of fish metabolism accumulated and phenomena of great complexity were uncovered, the original simple question was pushed into the background by a number of new and special problems, dealing with isolated features of fish metabolism. The importance of the study of such problems cannot be denied; however, the study of the conditions which determine the level of metabolism of each species of fish in its natural environment remains the ultimate goal of research in this field. It is data of this kind that are needed to solve problems that have come to the fore in fishery management.

Bearing this in mind, we have concentrated our attention upon the results of the measurements of the rate of metabolism, setting to one side its physiological and biochemical mechanisms. This can be done because the morphological and physiological peculiarities of various species of fish must have developed in such a manner, during the process of evolution, that in the environment which is normal for each species (that is, under the conditions to which it has become adapted) it can maintain a certain level of metabolism needed for normal development. This problem is solved by a great variety of physiological mechanisms, depending on the structure, manner of life, local conditions and biological peculiarities of each species. It is not the existence of a particular kind of structure of the organs of respiration, blood circulation, or what-not that determines the metabolic rate; rather, the metabolic requirements of a particular way of life and place of abode determine the development of such morphological and physiological characteristics in the fish as are dictated by the need for providing the necessary rate of supply of oxygen and the removal of carbon dioxide or other metabolic products.

These considerations indicate the theoretical possibility, and in fact the necessity, for a special treatment of the rate of metabolism as a definite and very important aspect of the process of metabolism. The possibility and usefulness of such a treatment of the question is supported also by the entire material cited in subsequent chapters and by the conclusions and generalizations based upon it. It is nevertheless quite clear that by limiting ourselves to a study of the quantitative aspect of fish metabolism, and refraining from any analysis of the physiological mechanisms which make metabolism possible at a particular rate, we have greatly narrowed the scope of the problems to be studied and of the possible conclusions. However from my point of view the path chosen was unavoidable, partly because inclusion of questions concerning physiological and biochemical mechanisms of respiration in fish [page 5] would require a book two or three times the size of this, but also for more fundamental reasons. At the present level of knowledge it is not yet possible to relate the differences in the metabolic rates of different fishes definitely to any concrete physiological and biochemical characteristics. This can be done in a few cases, but only with respect to particular manifestations of ecological and physiological differences--for example, greater or less resistance to asphyxiation as related to the properties of the hemoglobin. But as a matter of fact, even in the few cases that have been studied we are very far from understanding how the processes take place in the body of the fish, or the conditions and circumstances which determine why an experimental subject has a particular metabolic rate.

The information at hand permits us only to set forth some of the most important problems whose solution is necessary for an understanding of the physiological mechanism that determines a particular metabolic rate. However, in view of the present development of comparative physiology, a fruitful study of such questions as, for example, the interrelation of tissue metabolism and the metabolism of the entire organism, the connection between the properties of the hemoglobin and respiration, or the physiological basis of different forms of relationship between respiration rate and the ambient partial pressure of oxygen, etc., cannot be made from data obtained in experiments on fish alone. Such a restriction would be entirely artificial. When solving such problems of a general physiological nature it is necessary to make use of all the pertinent data, rather than selecting them on the basis of the systematic position of the subjects from which they were obtained; although the latter, of course, has to be taken into consideration. Thus if the physiological mechanism of of respiration were included in the study, we could only to a slight degree and in rare cases connect it causally with so general a parameter as the rate of metabolism, which sums up a whole complex of morphological and physiological properties of each organism. Furthermore, the necessity would arise either to enlarge the scope of the phenomena to be studied to indefinite limits or, limiting oneself to information obtained from fish, to treat important general physiological questions artificially and even superficially.

Finally, and this is of no less importance, the study of the quantitative aspect of metabolism is carried out using methods peculiar to itself. Also, the processing and interpretation of data pertaining to the quantitative aspect of metabolism require special procedures. As shown below, in the actual conduct of research it often happens that this aspect of the problem is underestimated; not enough attention has been given to obtaining appropriate parameters that really reflect the metabolic rate for fish [page 6], or to the quantitative formulation of relationships that link metabolic rate with the various characteristics of the experimental material or the environmental conditions. Consequently it has seemed necessary to give special treatment to this rather clearly defined field in the ecological physiology of fish, which has its own objectives and methods of study.

Metabolic rate in fish, as in other animals, is most often evaluated by the rate of respiration, chiefly by the rate of oxygen consumption. The rate of oxygen consumption of various freshwater and marine fishes has been studied by many authors. The use of published data is made difficult by the fact that they are of far from uniform value, having been gathered by diverse and not always reliable methods, and under different conditions. Many authors have overlooked important factors that influence a fish's metabolic rate; they do not give enough attention to the fact that the metabolic rate depends on how the fish were held prior to the experiment; and, what is particularly annoying, they have failed to give complete-enough descriptions of the conditions under which their measurements were made. For this reason some foreign research workers maintain that, in general, published data are inadequate for estimating the true value of the metabolic rate. On this view, nothing is known for sure about metabolic rate among fishes (Black, 1951). It is shown below that it is impossible to agree with this pessimistic, even nihilistic, statement.

The composite tables of measurements of fish respiration rates, quoted in various reviews and manuals, represent the opposite extreme in points of view, but they too suffer from the absence of any critical analysis of the published material or synthesis of the empirical data.

Data on the metabolic rate of fish were compiled for the first time in the well-known review of Kestner and Plaut (1924), and later in the book by Leiner (1937). In both cases data of various authors were included in the tables without the slightest effort to critically appraise the accuracy of the different figures. These tables are very incomplete, or rather they represent a casual collection of some of the published figures. They include many unreliable data from early works, and they do not include a lot of recent and reliable material from foreign authors, not to mention the fact that Soviet literature is ignored completely. Measurements are presented that were obtained at different temperatures, that refer to fish of different sizes, and so on. These indiscriminately collected and heterogeneous data do not contribute to knowledge of what metabolic rates are typical of fish, [page 7] or how they are related to the nature of the animals or to [environmental] conditions. Even more eclectic and less representative are all those examples of fish metabolic rates which are cited in text-books of general and comparative physiology, in manuals of fish culture, and in various other publications.

For this reason we have had to refrain completely from using any of the tables so compiled, or other second-hand data, and have consulted the original sources. All the material used below has been taken directly from the works in which the measurements were originally published. Contrary to the pessimistic prediction of Black and other authors, a critical study of the published data has permitted certain generalizations which, in our opinion, are of definite theoretical interest and make it easier to use the data in solving various practical problems of fishery management.

Though valuable information can also be found in foreign literature, the works of Soviet authors contribute particularly to the understanding of the metabolic rate among fishes. Systematic research on fish respiration was started by S. N. Skadovsky in the Lomonosov State University in Moscow. Of the many papers published under Skadovsky's direction, those of greatest interest are N. S. Stroganov's work on the relation of the metabolic rate of fish to temperature, A. B. Lozinov's work on the relation between the metabolic rate of young sturgeons and the partial pressure of oxygen in the environment, and some others. The Laboratory of Fish Physiology in the Federal Research Institute for Lake and River Fisheries (VNIORKh), directed by T. I. Privolnev, is a second center for the study of respiration of fish. The investigations of Privolnev and his co-workers (S. V. Streltsova, N. D. Nikiforov, and others) have shed light on many aspects of the metabolism of fish as related to various practical problems of fish culture. A number of valuable experimental studies of fish respiration have been carried out in various laboratories by individual research-workers. Most of these are in one way or another connected with the school of S. N. Skadovsky (V. S. Ivlev, A. P. Shcherbakov, V. I. Olifan, E. A. Veselov and others).

It is well known that the rate of oxygen consumption is not only the most widely used and accessible but also the most meaningful index of metabolic rate. This is particularly true of organisms living in water. Oxygen dissolved in water can be measured without any difficulty, but the measurement of carbon dioxide in water is considerably less accurate by the methods commonly used. Furthermore, in many cases the results of measurements of the rate of release of carbon dioxide by water organisms are obscured by [page 8] such phenomena as the partial solution of carbonates from their integuments, retention of carbon dioxide in the tissues, and so on. All this complicates the task of obtaining of reliable values of the respiratory coefficient for fish. The difficulties of determining accurately the respiratory coefficient of aquatic organisms have often been underestimated, especially in earlier works. Many attempts have been made to interpret differences between respiratory coefficients obtained from short-term experiments, when as a matter of fact the reality of the differences themselves is very questionable. It must also be stated, and this is a great pity, that some very recent works do not take into consideration the experience gained from earlier research in respect to the difficulty of obtaining reliable values for the respiratory coefficient of fish. For instance, G. N. Bogdanov and S. V. Streltsova (1953) give two tables of respiratory coefficient values for various fishes, without any indication of the methods used to obtain them.

The values of the 23 coefficients which they quote fluctuate within the limits 0.4 to 1.63 without any kind of order or sense! The authors, basing everything upon only one determination at each temperature, and not paying attention to the fact that the values of the respiratory coefficients they obtained cannot have any physiological meaning, are nevertheless quite unperturbed when they write that "Bream are characterized(!) by a very small respiratory coefficient at a temperature of 0°, which increases to 1.63 at 20°", and similar statements. Such carelessness with regard to method and so uncritical an attitude towards the results of individual measurements are astonishing. Even such an absurd value for the respiratory coefficient as 1.63 did not arouse any doubt in the authors' minds or prompt them to attempt to bring this value into line with generally accepted physiological concepts. It is obvious that respiration with a respiratory coefficient of 1.63 cannot continue for any length of time. Even if, during a short-term experiment, a respiratory coefficient did reach this high figure, it cannot be of any general interest.

It is still more difficult to bring the statement of T. I. Privolnev (1954) into accord with generally accepted physiological concepts when he says that "the respiration of crucian carp of 250-300 g, at a low oxygen content and a water temperature of 20°, is such" that in the absence of oxygen in their environment they give off 40-138 mg of carbon dioxide per hour per kilogram of body weight. Apparently here he is speaking of observations made during the brief period of incipient asphyxiation prior to the death of the fish, when carbon dioxide is released from the alkali reserve as a result of acidification of the environment from glycolysis and other processes of anaerobic metabolism. But how is the following paragraph in the same article to be understood? "In the winter of 1952 fingerling crucian carp weighing 7-10 g were placed in hermetically [page 9] sealed glass respirometers of a capacity of up to 500 cc. Some of these fish survived for more than 2 months on the oxygen that was in these chambers at the beginning of the experiment (about 4.5 mg), the water temperature being 3-8°. The main bulk of the oxygen was consumed by the crucian carp during their first hours in the respirometer. The rest of the time (more than 2 months) they lived by means of anaerobic processes taking place in their body" (page 45). We will not undertake to comment on this astonishing statement, apparently unique in contemporary physiological literature, which affirms the ability of a vertebrate to maintain active life for a protracted time under conditions of strict anaerobiosis. We will only mention that recently there has been some reason to doubt the ability even of intestinal parasites, in whose metabolism anaerobic processes play a large role, to maintain active life for a protracted period under strictly anaerobic conditions (Winberg, 1948).

The very first thorough work on fish respiration (Jolyet and Regnard, 1877) showed that the respiratory coefficients of fish under ordinary conditions in no way differ from the coefficients known for other representatives of the animal kingdom. It is characteristic of early authors that they paid much attention to the respiratory coefficient of fish, whereas recent authors commonly limit themselves to measuring the rate of oxygen consumption. In a majority of cases this is quite sufficient.

It is possible to calculate energy consumption in metabolism sufficiently accurately from the rate of oxygen consumption, independently of the size of the respiratory coefficient. Indeed, let us take the limiting possible values for the non-protein respiratory coefficient, 1.00 when fed exclusively with carbohydrate and 0.718 when fed exclusively with fat. The corresponding oxycalorific coefficients will be 5.047 and 4.735 Calories [kilogram-calories] per liter of O_2. Even these extreme values deviate by only ±3.5% from their mean. For ordinary values of the respiratory coefficient, the deviations from the mean do not exceed ±1.5%. Neglecting the protein metabolism will not introduce any significant error. It can be shown (Weir, 1949) that the energy expenditures calculated from the non-protein respiratory coefficient should be reduced by only 1% for every 12.3% of the total metabolism allotted to protein.

It is often forgotten that even with the most "exact" calculations of the energy aspect of fish metabolism, figures must unavoidably be used which from their very nature are provisional to a considerable degree, and which have been obtained from experiments on completely different animals. By the great expenditure of labour required for determining nitrogen metabolism and the respiratory coefficient, it is possible to obtain [<u>page 10</u>] a small (1-3%) and purely illusory increase in the "accuracy" of the figure for energy expenditure.

Fish, like other cold-blooded animals, do not have a definite stable basal metabolic rate. For this reason the metabolic rate of fish can only be obtained by a rather large number of separate measurements. Often this (it would seem) well-known fact has been ignored, and the results of one or few measurements are used, not as approximate values, but as accurate ones; so that, without any justification, real significance is ascribed to small discrepancies, etc. In this connection, we have given much attention to applying to the material on fish metabolic rates the generally accepted methods for statistical treatment of quantitative data, endeavoring to test the authenticity of the conclusions by objective criteria.

The rate of oxygen consumption, like any other index of metabolic rate, does not completely reflect the quantitative aspect of the metabolism of different subjects; metabolic rate is, in fact, inseparably bound up with the specific peculiarities of each subject investigated, i.e. with the qualitative aspect of metabolism. One and the same rate of oxygen consumption can have a different physiological meaning in the case of a rapidly growing and in the case of a starving fish. S. N. Skadovsky (1939) was correct when he said that "an increase in the oxidation processes denotes an acceleration of the total metabolism only if it is accompanied by a corresponding increase in the assimilating function of the organism and is associated, at any particular stage, with a normal increase in growth and development."

The imperfections and provisional character of all methods for the quantitative study of the metabolic rate of fish do not remove the standing need to discover what laws prevail in this realm. At present this can only be done by studying the material on rate of oxygen consumption of fish; as it is only for that datum that sufficient material is available.

This book contains a collection of the data that are available concerning the oxygen consumption of fish, presented in such a way as to facilitate comparisons. This has made possible a number of generalizations which help to reveal the nature of the relationship of metabolic rate to environmental conditions, to the general size of the body of the fish, to the peculiarities of different species, and so on. This in turn opens up new possibilities for calculating the food requirements of fish and for solving other problems directly associated with practical fish management.

2. Methods of measuring the metabolic rate of fish

Measurements of the rate of oxygen consumption of fish have been made by various authors who have used diverse methods, but the majority belong to one of three main types: the sealed vessel method, the gas recirculation method, and the flowing water method.

The simplest method, using closed vessels, was used in the first attempt to study fish respiration (Humbolt and Provençal, 1811). It consists of the following: one or several fishes are placed in a measured amount of water, which is isolated from atmospheric air. Before and after a definite exposure time, the oxygen content of the water is measured and the amount of oxygen consumed is ascertained from the difference between these two determinations. This method is still successfully employed by many authors. When properly and cautiously applied it still yields excellent results. The well-known data of Ege and Krogh (1914) can serve as an illustration; they discovered the "normal curve" relationship of rate of oxygen consumption of goldfish to temperature by this method.

In order to insulate their fish from the atmospheric air, some authors (Pereira, 1924; Heé and Bonnet, 1925; Toryu, 1928; Gompel, 1937; Shlaifer, 1938; Oya and Kimata, 1938) placed them in water below a layer of mineral oil. At first it was assumed that perfect separation had been achieved in this way. Later it was proved that oxygen passes through oil at an appreciable rate (Allee and Oesting, 1934). Nevertheless, oil greatly reduces the rate of gas exchange with the atmosphere. Therefore, if there is a sufficiently rapid reduction of the oxygen by the respiration of the fish, as usually happens when such measurements are made, the rate of oxygen consumption under these conditions can be established with little error. In other cases, however, the use of this very primitive method has entailed gross errors. At the present time isolation from atmospheric air is achieved in most cases by placing the fish in hermetically sealed calibrated vessels (Ermakov and Medvedeva, 1924; Adrianov, 1937; Brîukhatova, 1939; Ivanova, 1939; Stroganov, 1939; Maksudov, 1940; Privolnev, 1946; Taliev, 1947; Maksudov, 1948; Markova, 1949; Kharchenko, 1949; Tauson, 1949; Yablonskaîa, 1951; Lozinov, 1952, 1953; Ivlev and Ivleva, 1952; Mints, 1952; Winberg and Khartova, 1953; Ivlev, 1954; Vernon, 1895; Buytendijk, 1910; Henze, 1910; Pütter, 1909; Montuori, 1913; Ege and Krogh, 1914; Baldwin, 1923; Baudin, 1930-1932; Terroine, 1931; Raffy, 1933; Sumner, 1942; Hasler, 1942; Leach, 1946; Fry and Hart, 1948; Schlieper, 1952; and many others).

[page 12] In the simplest and most widely used form of the sealed vessel method, it is possible to determine only the total oxygen uptake during the course of the experiment. It is impossible to detect possible variations in rate of consumption during the experiment. In order to obviate this shortcoming some authors have used siphon-equipped glass jars. With these it is possible to obtain samples of water for analysis, while replacing it with the necessary amount of water (Lozinov, 1952, 1953; Fry and Hart, 1948). A. G. Mints (1952) replaced the siphoned-off water with hydrogen. She assumed that in this way the error which would arise from absorption of oxygen from the air would be avoided. It can easily be seen that replacing air with hydrogen in no way reduces the magnitude of the possible error; but merely reverses its direction. When, as is usual, the oxygen saturation of the water exceeds 50%, replacing air with hydrogen only increases the difference of oxygen pressures between the liquid and gaseous phase; and the error from loss of oxygen from the water into the hydrogen will be greater than the error that would arise (under the same conditions) from the enrichment of water with oxygen from the air.

The method of Maloeuf (1936, 1937) is an ingenious and peculiar modification of the sealed vessel method, in which the water taken for samples is replaced by mercury.

When there is little motion of the fish in the respirometer during an experiment, the oxygen content in the immediate proximity of the experimental fish can become greatly reduced. Thus the average oxygen content in the vessel in such cases will not correctly represent the conditions to which the animal was exposed during the experiment. N. S. Stroganov (1939) and also Lindroth (1942) used special vessels that were equipped with stirrers to circulate the water.

In another interesting modification of the method, a current of water is set up in a special revolving ring-shaped vessel, which makes it possible to measure the rate of oxygen consumption of fish swimming at different rates (Fry and Hart, 1948; Graham, 1949). For the same purpose L. A. Kovalevskaîa (1953), in V. V. Shuleĭkin's laboratory, used a vessel in which a circular water current was set up by means of a propeller.

The universally accepted Winkler method is usually used in determining the oxygen content of the water. Only a few authors resort to different methods of analysis, such as potentiometric determinations (Hasler, 1942) or the Van Slyke method (Toryu, 1928; Maloeuf, 1936, 1937). It was pointed out (Allee and Oesting, 1934) that under certain conditions, as a result of the presence of the fish in the respiratory [page 13] vessels, there is an accumulation of nitrites, in the presence of which the Winkler method gives values slightly too high. To remove this error the Rideal-Stewart method was recommended, and has been used by some authors (Ivanova, 1939; Maksudov, 1948; and others). However, it became evident that when measurements are made under ordinary conditions the nitrite error is not appreciable (Wells, 1935; and others). It seems that this error can occur only in special circumstances, for example after a large number of freshly fed fish have spent some time in the vessels--something which is usually avoided when measuring the rate of oxygen consumption. Recently it was proven by carefully conducted experiments that if the usual conditions for measuring fish respiration are observed the Winkler and Rideal-Stewart methods give identical results (Fry and Hart, 1948).

In works published prior to the development of the Winkler method, the oxygen content of water was determined by vacuum extraction of the gases (Gréhant, 1869, 1886) or by boiling (Vernon, 1895), followed by analysis of the gas.

The main advantage of the sealed vessel method is that it is simple and can be used under any conditions. Its chief defect is the impossibility of creating strictly constant conditions during the whole time of measurement. Throughout the time of exposure the oxygen is reduced in the respiration vessel, while the amount of carbon dioxide and of other products of metabolism increases. However, under ordinary conditions, this fact does not have much effect on the measurements, seeing that an accumulation of several milligrams per liter of carbon dioxide does not affect the metabolic rate, while the oxygen content of the water begins to affect the metabolic rate of fish only after it has dropped below a certain level (see below). This is taken into consideration by an overwhelming majority of authors, who have used vessels of such volume that the reduction of the oxygen content towards the end of the experiment would not exceed a third of its initial value.

The second method, the gas recirculation method, is the most complicated method technically. It is based on the well-known Regnard method for the study of respiration of terrestrial animals. The principle of the Regnard method was applied to fish by Jolyet and Regnard (1877), who measured the metabolic rate of a number of freshwater and marine fishes by means of it. The data of these authors were given wide publicity. The method of gas recirculation consists of pumping air or a gas mixture through the respirometer containing the fish and through a system of carbon dioxide absorbers, all in a closed circuit. The oxygen removed [page 14] by the fish is replaced by the addition of measured amounts of that gas. This method makes possible a simultaneous determination of the rate of oxygen consumption and of the rate of carbon dioxide excretion. Later the method of Jolyet and Regnard was applied and somewhat simplified by Bounhiol (1905), who used it to measure the metabolic rate of a number of kinds of marine fishes. The results of the careful measurements by Bounhiol, which were published in a journal of limited circulation, are not as well known as the earlier and less reliable data of Jolyet and Regnard, which have invariably been quoted up to recent times.

The extensive investigations by German authors of the school of the physiologist Zuntz are also based upon the gas recirculation principle. These deal with the study of the respiration and nitrogen metabolism of carp and other freshwater fishes (Knauthe, 1898; Lindstedt, 1914; Zuntz, 1901; Gronheim, 1911; for a drawing of the Zuntz apparatus, see Wundsch, 1937). An analogous method was used in Bucharest by Calugareanu (1907) in studying the unique characteristics of the respiration of the eel. Finally, as far as I am aware, the method of recirculation was last used in 1914-1922 to study the influence of the partial pressure of oxygen upon the rate of oxygen consumption by fish (Gardner, 1926).

Since that time the method has no longer been used, not only because of its great complexity, but also because it is not free from serious shortcomings. In using it, reasonably accurate measurements can be made only on large fish, or on a large number of small fish placed in the apparatus at the same time (in his experiments Lindstedt put 265 perch weighing 3904 g into a vessel with a capacity of 52.7 liters!). During the experiment the fish move about, since they find themselves in a vessel through which air is passing. Considerable distortion in the results of prolonged experiments can arise because the water in which the fish are living is not changed and bacteria develop in it. It is difficult or even impossible to check the rate of oxygen consumption during the course of the experiment. It is very important that the fish are in motion when making measurements by this method, for fish of different species possess different degrees of mobility and excitability, and behave very differently during the measurements, making it very difficult to obtain comparable material.

The flowing water method is free from these defects and is also simpler and more refined. It makes it possible to measure the rate of respiration of a single specimen of fish of any size, to watch the rate of oxygen consumption during the experiment and, what is of particular importance, to maintain a strictly constant environment throughout the experiment, as well as the immobility of the fish undergoing the test. The flowing water method for measuring [page 15] rate of respiration in fish was first used a long time ago (Gréhant, 1886). Afterwards it was used by Winterstein (1908) for his well-known work on the study of the physiology of gill respiration in fish. However, Winterstein fixed the fish and created a forced flow of water through the oral cavity and the gill slits, thus interfering with normal conditions of respiration. In the hands of A. Krogh (Ege and Krogh, 1914; Gaarder, 1918) this method assumed the simple form which it has retained down to the present. At first, in order to eliminate movement and to make it possible to measure "standard metabolism", the measurements of respiration in the Krogh laboratory were made on fish narcotized with urethane. It soon became evident that fish in a respirometer with flowing water will, as a rule, remain motionless for a long time without narcosis. For this reason subsequent authors have worked and still work with fish that are not narcotized.

The well-known work of Keys (1930) discusses the methods for the study of respiration of fish, and the flowing water method is recommended (see also Wells, 1932). Since that time this method has been used extensively, especially by American authors (Hall, 1929; Keys, 1931; Adkins, 1930; Wiebe and Fuller, 1933; Wells, 1935; Clausen, 1936; Oya and Kimata, 1938; Etkin et al., 1940; Smith and Matthews, 1942, 1948; Matthews and Smith, 1947; Freeman, 1950; also, independently of these workers, by Powers, 1923; Szarca, 1930; Geyer and Mann, 1939; Precht, 1951; Halsband, 1953; Schmeing-Engberding, 1953).

The flowing water method has also been used successfully by many Soviet authors. These are mainly of the school of S. N. Skadovsky (Svirenko, 1937; Shcherbakov, 1937; Ivlev, 1938; Novikova, 1939; Stroganov, 1949; Veselov, 1949).

The great advantages of the flowing water method are evident. However, this method also has its weak points. The rate of oxygen consumption is determined by the difference of the oxygen contents in the water before and after it passes through the respiratory chamber. The absolute value of this difference is small, so considerable error can creep in when calculating the rate of oxygen consumption. For this reason N. S. Stroganov (1940), after having had much experience in studying fish respiration, made an attempt to construct an apparatus which, in his opinion, combines the advantages of all three principal methods. By means of a pump he caused a certain volume of water to circulate from the respirometer to a reservoir [and back again, the reservoir being] equipped with a clever device by which it is possible to draw samples of water for analysis. However, we must observe that Stroganov's device, which is an improved and complicated variant of the sealed vessel method, does not eliminate the basic defect of that [page 16] method, the impossibility of maintaining strictly stable conditions. If the reservoir is large, the defect of the flowing water method, namely, poor accuracy in determining the amount of oxygen consumed, is not eliminated either. Furthermore, the data obtained by Stroganov when using this apparatus raise doubts concerning its suitability. It was discovered that on changing from a slow speed of water circulation to a somewhat higher speed, the rate of oxygen consumption of the fish also increased. Stroganov considers it possible to suppose that when the rate of the flow of water is increased the basal metabolism of the fish does actually increase also; and he is not at all worried that according to his data a sterlet, for example, following an increase in flow of only 0.06 m/sec, which is a very small amount, "increased its oxygen consumption 7 times"(!); and further, that at slow current speeds the sterlet in his experiment had a "metabolic rate" far below normal. In spite of all the lability of the metabolic rate of fish, it is nevertheless impossible that the metabolism of an immobile fish could vary over such a wide range. This, as well as the other peculiarities of the data in this work, leave no doubt that the change in the rate of the circulation of the water in the experiments by Stroganov produced only illusory changes in the basal metabolism of the fish.

It would seem that when the current flowed slowly, water with a low oxygen content stagnated in dead regions of the respirometer, which water was forced out by an increase in rate of flow. Wolsky (1934) pointed out that errors of this kind are possible when using the flowing water method. In order to prove a relationship between basal metabolism of fish and rate of the flow of the water, long experiments would be necessary to demonstrate at what particular stable level the metabolism of the fish becomes established, for different speeds of water flow.

It is also impossible to agree with the statements of Geyer and Mann (1939) who, disagreeing with other authors on the basis of very scant and completely unconvincing data, consider that the size of the respirometer affects the results of the measurements of the rate of oxygen consumption by fish. If there existed any such close relation of the metabolic rate of motionless fish to the rate of water flow as is assumed by Stroganov in his 1940 work, or any effect of size of the respirometer on the measurements, this would make the use of the flowing water method invalid, whereas practical experience with this method indicates the opposite.

Besides the three main methods, just described, for measuring the rate of the respiration of fish, other methods also have been used. Some authors, working with fry or small [page 17] fish, have employed different variations of manometric methods. Thus the Warburg apparatus was used by P. A. Korzhuev (1941) for fry and fingerling sturgeons, while T. I. Privolnev (1945, 1946) used it for the young of various cyprinids. Leiner (1937, 1938) determined the rate of oxygen consumption of the sea-horse and its young by means of the same apparatus. Smith (1943) used the same method to measure the metabolic rate of Lebistes. V. I. Olifan (1940, 1945, 1945a), and Yu. D. Poliakov (1940) used the Drastikh differential manometer when studying the rate of oxygen consumption by the young of various fishes. Other authors too have attempted to use manometric devices (Geyer and Mann, 1939; Haugaard, 1943) to study fish respiration. Many authors observe that during the first hours of an experiment the fish show an increased consumption of oxygen. This is usually ascribed to increased activity and excitement after being placed in the vessel. It is important to bear in mind that motor activity, which definitely affects metabolic rate, is not necessarily associated with clearly distinguishable movements; it can consist of barely perceptible ones--in which event the behaviour of the fish in the respirometer is described as quiet or "almost motionless". Halsband (1953) used the flowing water method for measuring the oxygen consumption rate of fish with excised pectoral fins. His data show that in fish that had not been operated on the respiration rate changed much more, with change in conditions, than the fish that had been operated on. This indicates that the motion of the pectoral fins has a noticeable effect upon the rate of oxygen consumption of fish. As early as 1925 Crozier pointed out that moving the pectoral fins accelerates the rhythm of the respiratory motion (Crozier and Stier, 1925).

Keys (1930) especially emphasizes the accelerated rate of oxygen consumption during the first period after the fish have been placed in a respirometer. According to his data, which were obtained from several species of saltwater fish, a gradual reduction in metabolic rate is observable during the early part of an experiment. A constant level of metabolism (the "standard metabolism") was established only after 3-4 hours in these experiments. It can be seen from Keys' charts that in the case of Fundulus, the original level of metabolism exceeds the "standard metabolism" by 50% during the first hour; in the case of Girella nigricans it is about 40%, for Clinocottus analis it is 70%. According to V. S. Ivlev's (1938) data the corresponding phenomenon is much less developed in carp. In them, metabolism during the first hour is not more than 20% above the standard level. According to data of Wiebe and Fuller (1933) the fry of largemouth bass consume oxygen during the first hours of an experiment at a rate 8-40% greater than in the subsequent period of stable [page 18] metabolic level. In order to obtain values for "standard metabolism" Keys recommends that fish be held first in respiratory vessels for at least 4 hours. Wells (1935) goes farther and considers that 24 hours are needed. With these data in mind a majority of authors, in using the flowing water method, begin their measurements only after a longer or shorter period of "familiarization" [privykanie] of the fish with conditions in the respirometer. On the other hand, only a few of the authors who use the sealed vessel method reject data obtained during the first hour, though this was done by Raffy (1933). An increased rate of oxygen consumption during the initial period of measurement is far from being observed in all experiments, or with all species. Nevertheless, this circumstance can be one of the causes of discrepancies between data obtained from the same species using different methods of measurement.

When measuring the respiration of fish, especially if they are small in size, frequently several specimens are placed in the respirometer, whereas in other cases the respiration of only one fish is measured. The question arises whether this circumstance can influence the result of the measurements. This question has already been the subject of special research, mainly by American authors of the school of Allee, who experimented with various invertebrates as well as with fish. It was first found for goldfish that if the number of fish is increased and the capacity of the respirometer remains the same, the oxygen consumption per fish drops (Schuett, 1934). Later, using the same subject, Shlaifer (1938) studied changes in degree of activity and in oxygen consumption in relation to the number of fish in the respiration chamber. According to his data, activity and oxygen consumption are somewhat higher for isolated goldfish, while if the capacity of the vessel is enlarged the difference in the behaviour between those kept singly and those in groups disappears. This author also maintains that in "conditioned water", i.e. water which prior to the experiment had contained fish, the rate of oxygen consumption is considerably lower than in unconditioned water, providing the level of activity [of the fish] is about the same. It is unfortunate that these important conclusions are based [page 19] upon a small number of measurements, which were carried out under inadequately controlled conditions and by means of the most primitive form of the sealed vessel method--that is, in aquaria covered by a layer of oil. In his second work, using the same method, Shlaifer (1939) showed that in the dark the metabolism of isolated fish does not differ from the metabolism of fish held in groups of four, and also that there is no "group effect" in the case of blinded fishes. On the other hand a "group effect" is manifested when there is visual contact with fish in an adjoining aquarium, or when a fish is placed in a mirror-walled aquarium. The data obtained are explained by Shlaifer on the basis of the greater activity of the fish which are not in visual contact with other specimens. The metabolic rate in the case of a "group effect", according to average data, is 25-50% lower than for a single fish. Wells (1935a), on the basis of a great many experiments on respiration of Fundulus, did not find that rate of oxygen consumption depends on the number of fish in the respirometer.

The experimental data available, while still inadequate, suggest that in species which display a clearly gregarious way of life, the degree of activity or of excitability, and consequently also metabolic rate, can change in the presence of other individuals. However there is, firstly, no reason to expect the same reaction in all fishes; on the contrary, the reaction should differ, it would seem, depending on the particular manner of life of the species in question. Secondly, if there is a reaction, it is primarily concerned with degree of activity, and could only indirectly and in small measure affect the metabolic rate of motionless fish.

The conditions under which fish are kept prior to an experiment are also of considerable importance. It is unfortunate that not only is there no uniformity in this respect, but even the origin of the experimental material and the conditions under which it was kept prior to the experiment are not always mentioned. Only with respect to feeding have most authors adopted the practive of measuring respiration 24 hours or more after the last meal; but even here there is not complete uniformity. The movements of fish during the period of measurement are of great importance to oxygen consumption. There is no doubt that this factor is the one most responsible for discrepancies between measurements of respiration obtained under otherwise identical conditions. The fish move least in experiments made by the flowing water method. When using the sealed vessel method the degree of mobility of the fish may differ greatly depending on the conditions. However, in practice, even in this case the fish in the respirometers are usually relatively quiet.

[page 20] For our purposes it is important to determine which of the methods makes it possible to obtain the most authentic values of the metabolic rate of fish. There is no doubt that each of the methods can provide fully reliable data if it is used properly. Ege and Krogh (1914) found that data

obtained by the sealed vessel method agreed well with those obtained by the flowing water method. The same thing has been found in very recent investigations (Privolnev, 1946; Oya and Kimata, 1938; Freeman, 1950).

The degree of reliability of the data of different authors does not depend upon what method they used, but on how closely they adhered to the conditions necessary for accurate results using the method chosen. It is unfortunate that the conditions under which measurements are made are rarely fully described. Sometimes not even the temperature at which the measurements were made is mentioned (Ermakov and Medvedeva, 1934; Fedorova, 1940; Privolnev, 1945; Buytendijk, 1910; Baldwin, 1923). This omission can be encountered even in the very latest works (Chertov, 1953).

In some instances this carelessness in the matter of method, or the ignorance of the authors, reaches such a pitch that the data they publish are so unreliable they cannot be taken into consideration at all (Baldwin, 1923; Pereira, 1924), although they have often been quoted uncritically by other authors. Unfortunately there is also an example, not altogether explicable, of such work being published in recent Soviet scientific literature (Markova, 1949). The degree of reliability of the data of different authors can vary greatly. It is not always possible to evaluate material from this point of view since the majority of authors fail to pay enough attention to this question. Only in very few works have the results of measurements been treated statistically, thus making it possible to discuss the reality of the differences under discussion on the basis of objective criteria. Another shortcoming in recent works is the fact that not enough use is made of the experience and results of previous research; this sometimes reaches extremes (Kharchenko, 1949). All this convinces me that the time is ripe for a review of the available material on metabolic rate of fishes, together with a critical comparison of this material, evaluation of the reliability of each set of data, and a generalization of the results obtained.

In order to be able to discuss the degree of reliability of published values for fish metabolic rates, it must first of all be discovered how metabolic rate changes with temperature, with partial pressure of oxygen, with the fish's physiological condition, [page 21] and other factors. This is examined in detail below. It was emphasized earlier that the purpose of this book is restricted to giving an account of and generalizing about quantitative data on fish metabolic rates and respiration in particular, since material on the rate of oxygen consumption is mainly used. In keeping with this main purpose of the book, the chapters in which the relation of metabolic rate to temperature and other factors are discussed serve primarily in an auxiliary capacity. They are directed toward explaining possible discrepancies between respiration measurements that result from the action of one or other of these factors. For example, data on the relation of metabolism to temperature are given primarily for the purpose of finding methods for comparing the material of different authors obtained at different temperatures. Because of this there is no need to study the relation of the metabolism of fish to temperature when the latter is close to 0° (below 5°). This is a particularly important question, which deserves special attention. Similarly, while we present the available data showing the general nature of the relationship between metabolic rate and the ambient oxygen content of the water (Chapter III), we will not dwell on the question of the conditions under which fish become asphyxiated. This important question, which is only indirectly connected with the main theme of this book, has a large and extremely contradictory literature, and requires separate treatment.

It must further be said that although material pertaining to both young fish and mature fish, of all ages and sizes, has been used, embryonic metabolism and metabolism during the first stages of post-embryonic growth (fish fry or larvae) will not be discussed. The material used concerning respiration of young fish refers primarily to the fully-transformed stages; although in a few instances data are discussed pertaining to metabolism at earlier stages of the development-ment--as shown in the appropriate tables.

The terms to be used to designate the different types or aspects of fish metabolism must be specifically defined. In view of the difficulties encountered when measuring basal metabolism [osnovoĭ obmen] or resting metabolism [obmen pokoi͡a] of poikilothermal animals, fish in particular, many authors follow A. Krogh and speak by preference of the so-called "standard metabolism" [standartnyĭ obmen]. Most often this term designates that more-or-less steady level of metabolism which is established by fish held for some time in a respirometer when respiration is being measured by the flowing water method. It is clear that when the fish, as usually happens, remain motionless for a long time and are not fed, the "standard metabolism" must be very close to the resting [page 22] or basal metabolism. However, when using data given in the literature it is rarely possible to judge whether, in each case, the conditions of measurement (even when the flowing water method is used) actually corresponded to those necessary to obtain the "standard metabolism". In general, it has not been established whether for all kinds of fish--rather than just those few that are favorite subjects for laboratory research--it is possible to obtain a constant level of "standard metabolism" that can be maintained for a long time. Therefore, there is neither need nor opportunity to make wide use of this term.

On the other hand, in discussing data it is impossible to avoid using the terms "resting metabolism" or "basal metabolism", which I regard as synonymous. The need for these terms, whose meaning is quite clear on the theoretical side, is not removed by the fact that in practice it is hard to define what figures actually represent the resting metabolism of a particular subject. Special attempts to determine, experimentally, values for the resting metabolism of fish are described in the appropriate places (pp. 96, 107, 171 and following).

It is obvious that when a fish moves, its metabolic rate increases. The majority of existing measurements have been obtained under conditions where motion of the fish was not completely prevented, and for this reason they must be somewhat greater than the "resting metabolism"; so in that sense they can be called "metabolism in the moving (active) condition" of the fish or, in brief, "active metabolism" [aktivnyĭ obmen]. In practice it is more useful to speak of "active metabolism" in cases where there are distinct movements by an actively swimming fish. The term assumes a definite meaning when both the rate of respiration and the rate of movement are measured at the same time (pages 168-179), especially if it is the maximum speed of movement and the corresponding maximum value of the active metabolism.

The great majority of published data on the metabolic rate of fish has been obtained, by the different methods, from subjects that were relatively quiet or almost motionless. There is no doubt that values obtained under such conditions are closer on an average to the "resting metabolism" than to the maximum possible value of the "active metabolism". However, they are not identical with the resting metabolism and therefore in discussing these data, there is a pressing need for a term indicating what kind of values are meant. Lacking a better alternative we have decided to use, in a purely formal sense, the term obychnyĭ obmen (page 150), which in a general way, perhaps, corresponds to the term "routine metabolism" that is sometimes used [in English].

[page 23] The speed of oxygen consumption and other indices of metabolism can be expressed by figures that refer either to the entire organism, or to a unit weight. In the latter case the metabolic rate is meant. It is clear that we must differentiate between the rate of resting metabolism, the rate of basal metabolism, the rate of routine metabolism, the rate of active metabolism, and so on. But if this terminology is strictly adhered to, our exposition will become extremely bulky. For this reason I consider that in many cases it is possible to write simply the "resting metabolism" or "active metabolism"; for the context should make it clear whether the rate of resting metabolism or the rate of active metabolism is really intended.

At times it is necessary to make use of figures that represent the amount of oxygen consumed during unit time by one fish.

When it becomes necessary to speak not of a rate of metabolism, but of values pertaining to the whole fish, I will use the term "total metabolism" [obshchiĭ obmen], for want of a better one.

Here, too, in the majority of cases it should be clear whether basal, routine or active metabolism is meant.

Regardless of the fact that the material at hand at the present time concerning the quantitative aspect of fish metabolism is inaccurate in many cases, or was obtained under non-standard conditions which make comparison difficult, nevertheless, as shown in the chapters to follow, it is quite possible to deduce from it a number of principles by which the quantitative aspects of the metabolism of fish are regulated, and to describe metabolic levels by quite definite figures.

Chapter II. [page 24]

The Relation of the Metabolic Rate of Fish to Temperature

1. General relationship between the metabolism of fish and temperature

The metabolic rate of fish, as of all poikilothermic organisms, is closely dependent on the temperature. Many authors have attempted to express the quantitative aspect of this relationship. As is well known, the researches of A. Krogh and his co-workers marked an important stage in the study of this problem. By means of experiments carefully conducted with organisms of very diverse systematic position (goldfish, frogs, flour beetle pupae, dogs) it was shown that the relation between the metabolic rate and temperature in motionless animals ("standard metabolism") is subject to a general quantitative law common to all groups, which can be expressed by what has been called "Krogh's normal curve" (Krogh, 1916).

The rate of oxygen consumption of a motionless goldfish follows this curve (Ege and Krogh, 1914). As time passed, "Krogh's normal curve" gained great popularity, and it was repeatedly confirmed by experiments done on very diverse material. However, critical comments were not lacking. Many authors, having obtained experimental results that deviated from the normal curve, expressed doubt as to the universality of the relationship described by it. In spite of this, when describing the relationship of metabolism of poikilothermal animals to temperature in his 1941 book, A. Krogh considered it appropriate to limit the presentation to a description of the origin of his "normal curve", without any qualifications (Fig. 1).

Can we agree with this? Is it really possible to establish a general law expressing the relation between fish metabolism and temperature? Let us examine the results of all the observations at hand in which fish metabolic rate has been followed over a sufficiently broad range of temperature. In order to compare the data obtained from subjects which have different levels of metabolism, all the results to be discussed are expressed as percentage deviations from the metabolic rate at 20°.

[page 25] The first thorough study of the metabolic rate of a number of representatives of the marine fauna, including the lancelet and two species of fish, conducted by Vernon (1895),

had already contained data describing the relation between the metabolism of poikilothermal organisms and temperature. In spite of the imperfect methodology of this early work, Vernon's data are quoted without fail in all the reviews, and have been mentioned in quite recent papers (Stroganov, 1939). For each of his experimental animals Vernon made only a few measurements at different temperatures. The irregular results obtained of course do not justify Vernon's conclusion, which now sounds naive, that "at all temperatures there are intervals over which metabolism remains constant". It is of interest that the average data for all 12 species of poikilothermal animals studied by Vernon result in a smoothly ascending concave curve, which is close to or practically coincident with the "normal curve" of Krogh.

[page 26] The relation between metabolism and temperature in the lancelet and the fish Serranus can be described perfectly by this average curve, whereas the results of 9 measurements of metabolic rate of the fish Heliases are better described by a less steep curve. However no real significance can be ascribed to this difference.

The data of Lindstedt (1914) have also been given wide publicity. They concern the relation of metabolism in the tench to temperature and are shown in Fig. 2, in the form used here. It is easy to see that the measurements made at 13-14° gave relatively high results. Some authors have thought it possible to ascribe special significance to this fact, and have seen in it a confirmation of their idea that there exist certain zones of temperature within which metabolic rate remains more or less constant (Clausen, 1933; Wells, 1935; Stroganov, 1939). In this connection, the fact has been overlooked that another important index of metabolic rate, namely the rate at which the nitrogenous products of metabolism are given off, contradicts this interpretation. This index, according to data in the same work, in no way suggests deviations from the "normal curve", as is quite evident from Fig. 2.

From further study of Lindstedt's work it is easy to see the reason for the relatively increased rate of oxygen consumption at 13-14°. The fact is that these data were obtained over the course of 2.5 months from a group of fasting tench. Furthermore, all the measurements at 13-14° were made at the beginning of the period of fast, whereas the measurements at 26° are the last. To explain all the peculiarities of the results obtained, it is sufficient to make the perfectly reasonable assumption that at the start of the fasting period the tench moved around more actively in the 52-liter respirometer used by Lindstedt.

[page 27] The data obtained by Gardner (1926) and his co-workers are often quoted. They are graphically depicted in Fig. 3, in which each point corresponds to one measurement.

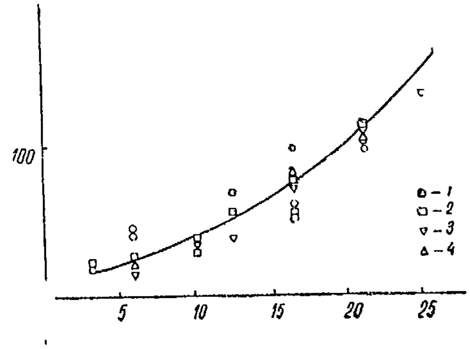

Fig. 3 [page 27]

Relation between the metabolic rate of fish and temperature, according to data of Gardner (1926). Axes as in Fig. 2.

1- trout; 2- grayling; 3- eel; 4- pike.

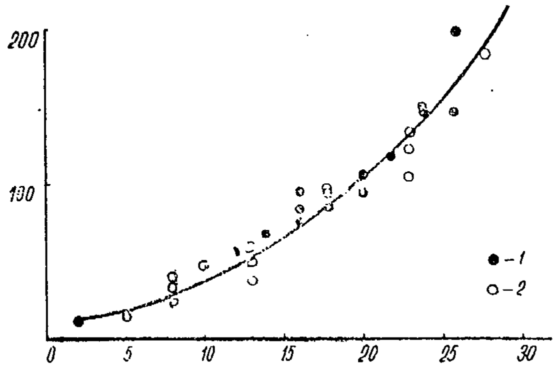

Fig. 4 [page 27]

Relation between the metabolic rate of *Fundulus parvipinnis* and temperature, from Wells' (1935) data. Axes as in Fig. 2.

1--first series of measurements (in winter; weight of one fish about 4.25 g); 2--second series (in summer; average weight of a fish about 5.3 g).

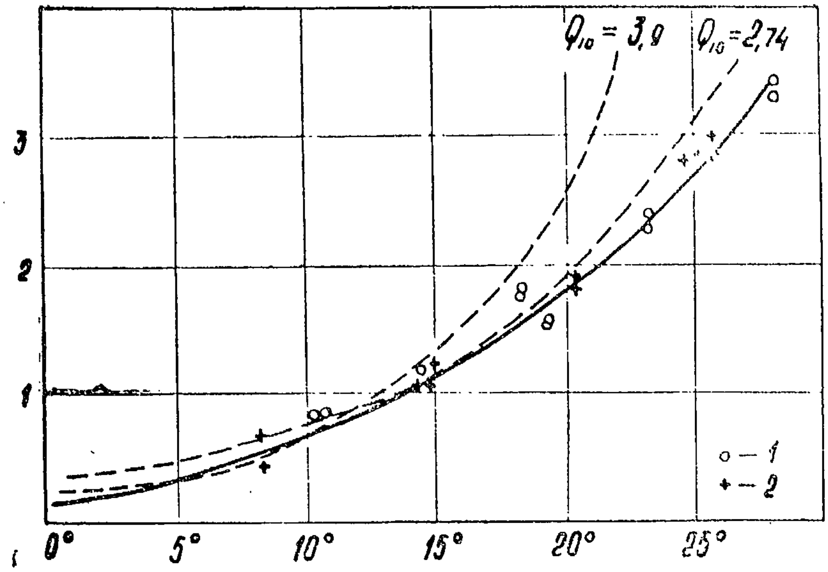

Fig. 1 [page 25]

Relation between the metabolic rate of fish and temperature, from data of Ege and Krogh (1914).

The ordinate shows the oxygen consumption of goldfish in ml O_2/kg/min. 1- fish narcotized; 2- fish not narcotized. Solid line--the "normal curve"; broken lines--curves for two constant temperature coefficients (3.9 and 2.94).

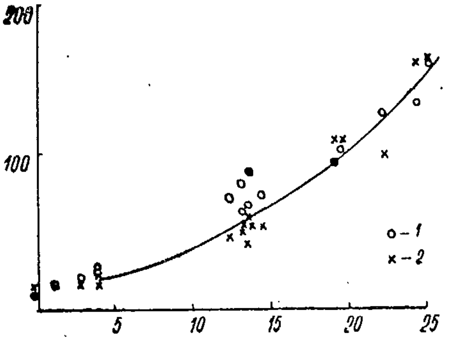

Fig. 2 [page 26]

The relation between the metabolic rate of tench and temperature, from data of Lindstedt (1914).

Ordinate--metabolic rate as a percentage of the metabolic rate at 20°; abscissa--temperature. 1- oxygen consumption; 2- nitrogen excretion. Curved line--the "normal curve" of Krogh.

All those who have had experience with measurements of metabolic rate of poikilothermal aquatic organisms, especially fish, know very well how large are the irregular fluctuations in measurements made under what seem to be identical conditions. Taking this into consideration, one must conclude that Gardner's data correspond to the normal curve of Krogh as well as they could. It is a curious fact that very recently one of the most thoughtful investigators of the metabolism of fish has used these data, or rather an arbitrarily selected portion of them, to demonstrate the inapplicability of the Krogh curve! (Fry, 1947, page 28, fig. 11).

On the other hand, Keys (1931) specially points out that his numerous and careful measurements of the rate of oxygen consumption by Fundulus parvipinnis, using the flowing water method, follow Krogh's curve exactly. For the same species, and using data collected at different seasons, this fact has also been pointed out by Wells (1935) in his widely familiar work devoted especially to the study of the relation of fish metabolic rate to temperature (Fig. 4).

[page 28] Very convincing materials concerning the question under study are contained in the works of N. S. Stroganov and E. G. Svirenko, carried out in Skadovsky's laboratory. By a number of especially carefully conducted experiments, Stroganov (1939) traced the rate of oxygen consumption of males, females and young of Gambusia holbrooki over a wide temperature range. His results are plotted in Fig. 5. With the usual scatter of the individual points, their general position in this case also can be perfectly well expressed by the same "normal curve". One can notice only a tendency toward a somewhat slower increase in the metabolic rate at high temperatures. A similar impression is conveyed by Fig. 6, on which are shown all the data obtained by Svirenko (1937, 1949) in studying the influence of temperature on metabolism of the sterlet. In this case it is noteworthy that Fig. 6 contains the results of several series of measurements made under very different conditions and in different years, and includes fish from fingerling size up to 355 g in weight.

Svirenko points out that in her experiments, even when conditions appeared to remain unchanged and the temperature remained constant, radical differences were observed in the results of consecutive measurements of the oxygen consumption by one and same fish. This phenomenon is well known. Nevertheless many authors, when discussing the relation of metabolism to temperature, fail to consider the possibility of random fluctuations in the data of different experiments conducted at different temperatures. In general, the relationship of fish metabolic rate to temperature is often interpreted very arbitrarily. Usually it is only an author's own (often quite inadequate) data that are taken into consideration, instead of the sum total of all [page 29] material available. If we consider also the other published material, which for the sake of brevity is presented here in graphical form (Fig. 7-13), the general character of the relation of the metabolic rate of fish to temperature becomes fully apparent.

In Fig. 7-13, 16 and 18 are presented, without selection, all the available data obtained by the various authors who have measured the metabolic rate of fish over a sufficiently wide range of temperature. Only Knauthe's data are excluded, which were obtained more than 50 years ago and later published by Cronheim (1911), who constructed from them those curves of the relationship between respiration and nitrogen metabolism in the carp that have often been reproduced in reviews and manuals. Actually this material is utterly unsuitable for this purpose. It suffices to say that Knauthe's measurements were made on a group of 4 fish over a long period of time (from April 24 to September 28), which explains many of the peculiarities of the results obtained. For example, it is quite natural that at a temperature of 14-17° relatively high values were obtained because the measurements at this temperature were made at the beginning of the period of observations; thus there are no adequate grounds for speaking of seasonal fluctuations in the metabolic rate, as Cronheim did.

[page 30] Very important results have been obtained by Scholander et al. (1953), who established particularly the relation of metabolic rate to temperature for tropical and arctic fishes. It was shown that the metabolic rate of 4 species of tropical fishes studied over the range 15-35° follow the "normal curve" beautifully. Four species of arctic fishes, whose respiration was studied from 0° to 15°, yielded lower values for temperature coefficients than was expected for these low temperatures according to normal curve.

The materials shown in Figures 2-13, 16 and 18 were obtained by a number of authors who used different methods for measuring the metabolism, and they concern fish of the most diverse systematic position, size and age, dwelling under the most varied conditions in fresh and salt waters. In spite of this there is not a single case in which the results of the measurements deviate appreciably [sushchestvenno] from the "normal curve". The more careful the technique used to obtain the data, and the more reliable the results of the measurements, the more closely do the empirical data follow the normal curve. This rather remarkable fact leads inexorably to the conclusion that Krogh's normal curve expresses the general law relating fish metabolic rate to temperature quite nicely.

Attempts to discover a universal formula or curve which would "exactly" express the relationship between the rate of biological phenomena [page 31] and temperature have forever receded into the past. There can be no expectation that experimental data will in every case strictly follow the

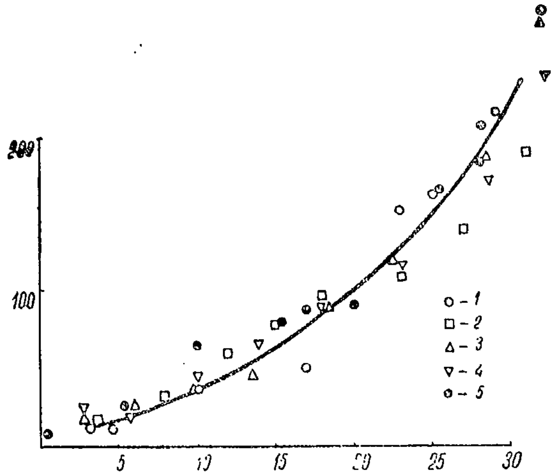

Fig. 5 [page 28]

Relation between the metabolic rate of fish and temperature, from the data of N. S. Stroganov (1939, 1939a). Axes as in Fig. 2.

1-4--Gambusia: 1- virgin females; 2- pregnant females; 3- males; 4- young. 5--perch. The points are the results of individual measurements.

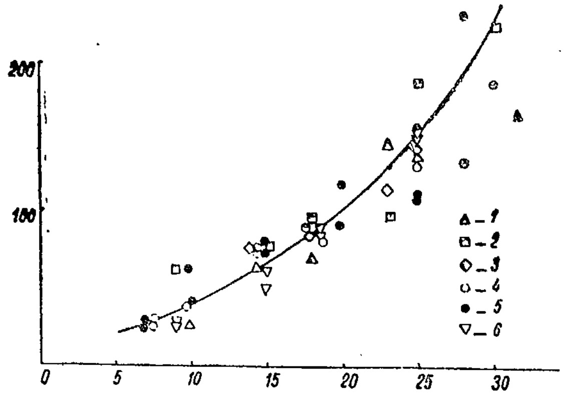

Fig. 6 [page 29]

Relation between metabolic rate of the sterlet and temperature, from data of Svirenko (1937, 1948). Axes as in Fig. 2.

1- fish No. 6; 2- No. 5; 3- No. 8; 4- No. 3 and No. 4; 5- fingerlings; 6- No. 7. The points represent the results of individual measurements.

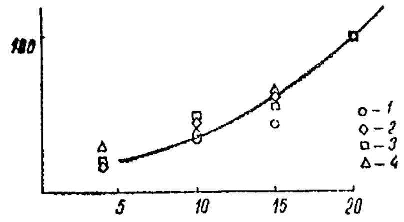

Fig. 7 [page 29]

Relation between metabolic rate of fish and temperature, from data of G. N. Bogdanov and S. V. Streltsova (1953). Axes as in Fig. 2.

1- bream; 2- perch; 3- zander; 4- pike.

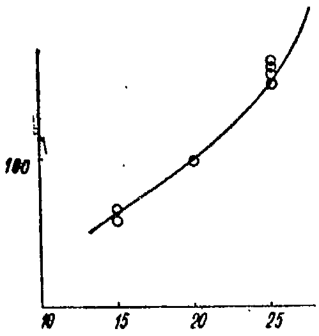

Fig. 8 [page 30]

Relation between the metabolic rate of *Huro floridana* and temperature, from the data of Wiebe (1933). Axes as in Fig. 2.

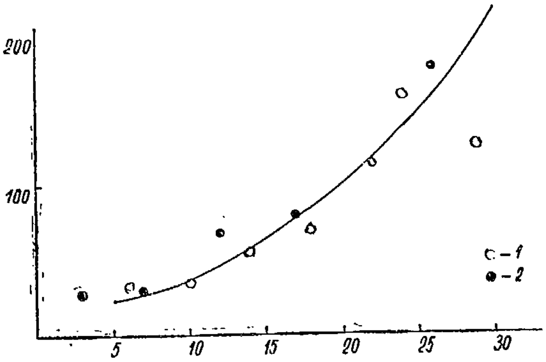

Fig. 9 [page 30]

Relation between metabolic rate of eels and temperature, from the data of Raffy (1933). Axes as in Fig. 2.

1- eel fingerlings (weight about 0.2 g); 2- eels weighing about 40 g.

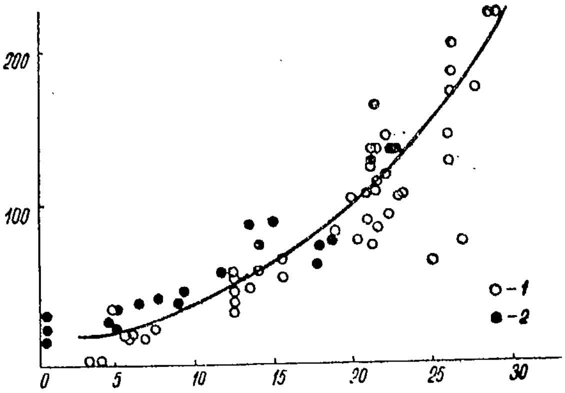

Fig. 10 [page 31]

Relation between the metabolic rate of Tautogolabrus adspersus to temperature, from data of Haugaard (1943). Axes as in Fig. 2.

1- summer material; 2- winter material. The points represent results of individual measurements.

normal curve or some other universal law, independently of prevailing conditions and peculiarities of the specific organism in question. However, experiment has shown convincingly that, in spite of this, the general character of the relation between metabolic rate of various animals [and temperature] can be expressed, as a first approximation and with sufficient accuracy for practical purposes, by the empirically-obtained normal curve.

Of course the "normal curve" can only serve for initial orientation, but for this purpose it is completely suitable and very useful. It makes possible rather accurate comparisons between measurements of metabolic rate made at different temperatures, by adjusting all the figures for metabolic rate to one temperature, let us say to 20°. Obviously [page 32] only approximate values can be obtained in this way. However, in using this method in practice one becomes convinced that it affords quite realistic results.

As is well known, the purely empirical "normal curve" has no logical basis. It cannot be expressed by a simple equation of any sort, such as would facilitate calculations when adjusting metabolic rate to a single temperature. The "normal curve" is described approximately by the following values for the temperature coefficient (Q_{10}):

Temperature intervals:	0-5°	5-10°	10-15°	15-20°	20-25°	25-30°
Q_{10}	10.9	3.5	2.9	2.5	2.3	2.2

Probably it would be better to take $Q_{10} = 2.0$ or 1.8 for the 25-30° range. It is possible to bring the data obtained to a standard temperature within the limit of each interval in question by using the above temperature coefficients and the usual formula:

$$K_2 = K_1 \times Q_{10}^{\frac{t_2-t_1}{10}}$$

The computations are rather cumbersome, especially in the case of wide temperature intervals; for this reason it is advantageous to present a table of the multipliers:

$$Q_{10}^{\frac{t_2-t_1}{10}}$$

These greatly facilitate the adjustment of values of metabolic rate to 20° (Table 1). In the practical use of the Table it is possible, by linear interpolation, to find multipliers for intermediate (fractional) values of temperature also, for example, 15.1°, 15.2°, etc.

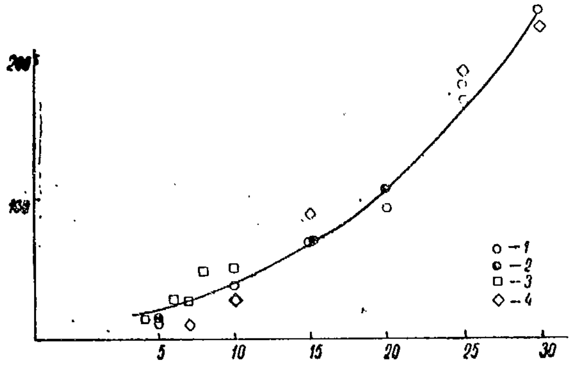

Fig. 11 [page 31]

Relation between the metabolic rate of goldfish and temperature. Axes as in Fig. 2.

1 and 2---data of Fry (1947), obtained from fish acclimated beforehand to the temperature of measurement. 1- motionless fish; 2- metabolism when in motion. 3 and 4--from the data of Baudin (1931).

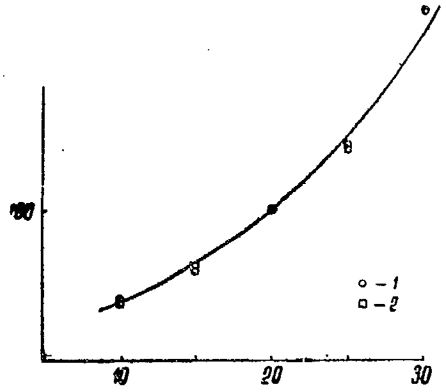

Fig. 12 [page 32]

Relation between the metabolic rate of carp and temperature. Axes as in Fig. 2.

1- data of V. S. Ivlev (1938); 2- data of Oya and Kimata (1938) (averages from their fig. 6).

cal data will deviate from the normal curve.

Here we enter a realm that has been little explored, and about which there is as yet a lack of concepts sufficiently developed or generally accepted. The use of published material and ideas is hampered considerably by the fact that a majority of authors who have interpreted the peculiarities of the results they obtained have failed to prove that it is not just a matter of accidental deviations involving only that particular experiment, i.e. they have not taken sufficient care to demonstrate the reproducibility of their results. Without that, all interpretations of the causes of any particular shape of the curve lose any objective significance they might have.

Many authors have expressed the opinion that empirically obtained curves of the relation between temperature and metabolic rate of various poikilothermal animals, including fish, have a flattened or even horizontal sector. This means that over some intermediate range of temperatures there is little change in the metabolic rate. This phenomenon was described for insects by I. V. Kozhanchikov. E. Ya. Graevsky (1946) reported it for aquatic pulmonate mollusks. These authors believe that the flattened sector of the curve lies within the range of optimal temperatures [for the animal in question].

Clausen (1933) too, when tracing the relation between rate of oxygen consumption by fish and temperature, found [page 35] in his experiments that at 15° the rate was lower than at 11°. From this result, which I regard as strictly accidental, he suggested that there is "nervous regulation" of metabolic rate. It is interesting that to support the existence of a flattened sector in the curve Clausen, as well as some more recent authors (Wells, 1935; Stroganov, 1939), refer to the data of Lindstedt (1914), the peculiarities of which actually have a much simpler explanation, as was shown above (page 26).

Wells (1935), as mentioned before, showed that data on the metabolic rate of Fundulus parvipinnis, obtained at various temperatures and at various times, follow the "normal curve" very nicely (Fig. 4). However, with the very same species, by means of a special prolonged series of measurements during which the temperature was only slowly and gradually changed, Wells obtained curves which, in his opinion, have flattened sectors at intermediate temperatures. These data have attracted attention and have been quoted repeatedly as proof of the existence of a flattened sector on the curve relating temperature to metabolic rate. However it is easy to show [page 36] that they do no such thing. Each of the three series of observations conducted by Wells was continued for more than two and, in one case, for more than three 24-hour periods. Superimposed on the gradual increase in temperature were the changes in illumination and other conditions that follow the rhythm of day and night. Fry (1947) drew attention to this circumstance, and presented Wells' data on a graph with the individual measurements plotted in sequence (Fig. 14). As a result, the influence of the diurnal periodicity on the rate of oxygen consumption becomes quite clear, and completely explains the mysterious flattened sectors on Wells' curves.

N. S. Stroganov gave much attention to the study of the relation of fish metabolic rate to temperature. He conducted a number of carefully designed experiments on this problem (1939, 1939a, 1940). From this research he arrived at very important conclusions concerning the nature of the relation of metabolic rate to temperature. When the data obtained with a gradually rising water temperature (not more than 1° per hour) are plotted, curves are obtained on which, in Stroganov's opinion, it is possible to detect flattened sectors. According to his interpretation, these sectors reflect a "temperature zone of adaptation" or "adaptive temperature zone". In his first work, in 1939, small perch were used. For the comprehensive work (1939a) specimens of the viviparous <u>Gambusia holbrookii</u> were used. In 4 series of measurements, the relation of metabolism to temperature was traced in young fish, in males, and in virgin and pregnant females. The rate of oxygen consumption was measured at each temperature, as was the rate of evolution of CO_2 and of ammonium nitrogen. Stroganov's curves which show the rate of production of CO_2 and of ammonia also have flattened sectors. However, the position of these sectors does not at all coincide with the position of the corresponding "zones of adaptation" for the rate of oxygen consumption. Moreover, if one turns to the respiration coefficients calculated by Stroganov, or the relations between rate of excretion of nitrogen and the rate of oxygen consumption, there remain no traces of the "zones of adaptation". Therefore it is hard to determine, from Stroganov's material, between what particular temperatures each "adaptive temperature zone" is actually located. The author fails to come to the reader's aid; he does not point out where, exactly, in his opinion, the adaptation zones are located, but contents himself with asserting that they exist, in a general way.

[<u>page 37</u>] Although it is difficult to recognize boundaries of adaptation zones from Stroganov's tables and figures, nevertheless it is plain that the curves obtained differ radically one from the other. This is in spite of the fact that all 4 groups of fish that were used in the experiment, with perhaps the exception of the first (the young), were held for a long time prior to the experiment under the same or very similar conditions. Seeing that each group was used for one experiment only, it remains unclear whether the same differences would have been obtained from repeated tests on one and

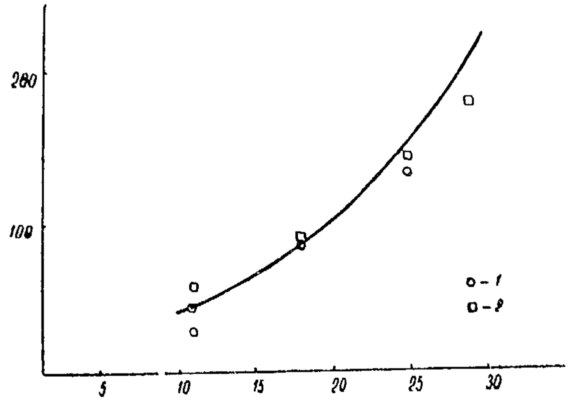

Fig. 13 [page 34]

Relation between metabolic rate and temperature for fingerling sevriuga and osëtr, from data of A. B. Lozinov (1950). Axes as in Fig. 2.

1- sevriuga; 2- osëtr.

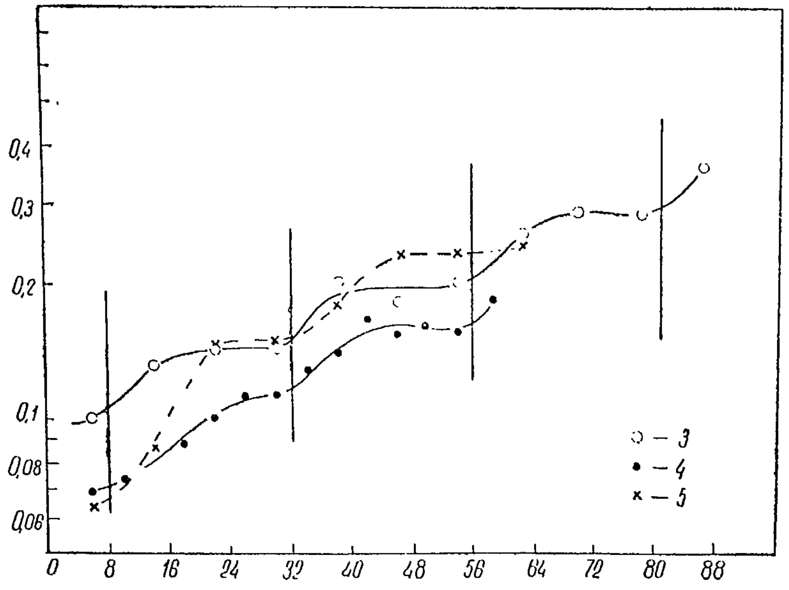

Fig. 14 [page 35]

The effect of diurnal differences in metabolic rate on the results of the measurements carried out by Wells (1935) in studying the relation of rate of oxygen consumption of Fundulus to temperature (from Fry, 1947).

Ordinate--O_2 consumption in ml/g hour (logarithmic scale). Abscissa--time in hours from the start of each of the three series of measurements. 3, 4, 5- numbers of the 3 series of measurements.

the same group of fish. Stroganov's (1940) very interesting and important statement, that the "zone of adaptation" for Gambusia living at a higher temperature is shifted in the direction of that higher temperature, is unfortunately not confirmed by any experimental material.

All Stroganov's data without exception, concerning oxygen consumption rate of Gambusia, are shown in Fig. 5. It is easily seen that the general course of the combined curve over a broad temperature range does not differ from the course which is usually observed in situations where the temperature changes rapidly. Consequently, summing the separate curves with flattened sectors does not lead to a flattening of the composite curve. This can happen only if the flattened segments of the partial curves correspond at the several temperature intervals, and disturb the normal form of the curve only in small sectors; that is if, of the two possible types of adaptation zone shown in Fig. 15, type A is realized. If however the separate curves, obtained during a slow change of temperature, differ from the normal curve in the manner of type Б, then the composite curve should be flatter than the curve obtained for rapid changes of temperature.

Quite recently an important study by Schmeing-Engberding, (1953) a student of Schlieper's, has been published. In this study the rate of oxygen consumption of fish at various temperatures is compared with the results of a study of the temperatures preferred by fish. According to these data, the oxygen consumption rate for all the species studied (trout, sculpin, goldfish, tench, carp) is practically independent of temperature over a small temperature range (1.5-4°), which varies with the species. [page 38] In other words, Stroganov's ideas were confirmed. It is of particular interest that he showed, using the same species, that the zone in which metabolism is independent of temperature actually coincided with the zone of optimal (preferred) temperature. Schmeing-Engberding mentions in his list of references the works of N. S. Stroganov, V. S. Ivlev, and A. P. Shcherbakov, but there is not a word about them in the text!

Schmeing-Engberding used the flowing water method. Prior to starting the readings the fish were kept in the respirometer for several hours, which, in his opinion, is long enough for temperature acclimation. Measurements were made every 1° or 2°. The fish were kept for 24 hours at each temperature. As far as I can tell from the incomplete description of the method and from the table of the results given for the metabolic rate of carp (as an example), the experiments were conducted with utmost care. Unfortunately all the measurements are presented only in graphs, and only in relative form--as percentages of the metabolic rate at the start of each preferred temperature zone. It remains unclear, when this method of exposition is used, to what extent the metabolic rate was really constant, because he says that metabolic rate was regarded as unchanged in cases where the measurements at two adjacent temperatures differed by up to 5% (but no more than that). Further, it is also unclear in what order the measurements were made, especially in the case of low temperatures. This is of primary importance in situations where the experiments continue for many days. An unfavourable impression is also created by the fact that the author repeats, without criticism, Schlieper's unfounded assertions about a difference between eurythermal and stenothermal forms in respect to the relation between metabolism and temperature--assertions that refer to very weak and inconclusive experiments. Very questionable, too, are Schmeing-Engberding's expansive deliberations about the various factors that influence fish metabolic rate, even including some "psychological" factors. All this greatly complicates the task of evaluating the reliability of the data of this paper.

It is most interesting that Schmeing-Engberding also measured the oxygen consumption rate of tench and goldfish that had been narcotized with acetone-chloroform. In both experiments there resulted an ordinary steadily ascending temperature curve, very close to the normal curve. No zones were observed in which metabolism was independent of temperature. If this is so, then one may assume that the apparent constancy of the metabolic rate at temperatures close to the preferred temperature occurs because temperatures below the preferred temperature stimulate the movement of the fish [page 39] and a reduction in metabolism is compensated by an increase in motor activity, with the net result that over a certain range metabolic rate is apparently independent of temperature.

One of the author's remarks is noteworthy, to the effect that in his experiments the narcotized fish had a higher metabolic rate than those which were not narcotized. This completely unexpected circumstance makes it possible to assume that in the regular tests, especially at higher temperatures, the metabolic rate of the fish was below normal for some [unknown] cause. Actually, the absolute data on metabolic rate, which are furnished only for the carp, show that up to a temperature of 21° the values obtained from this experiment correspond exactly to those expected from the data of other authors, but measurements at higher temperatures are considerably lower than the average metabolic rate that has been found for carp of the same size.

On the whole one must conclude that the very interesting views of Stroganov and other authors regarding the existence of zones of stability when temperature is changed slowly, which take the form of a flattened or horizontal portion on the curve relating metabolic rate and temperature, still require more work to provide them with a better foundation of factual material. In general, the course of the curves obtained experimentally is in each individual case determined

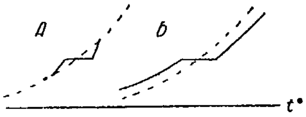

Fig. 15 [page 37]

Two possible cases of the effect of temperature acclimation on the curve of the relation of the metabolic rate to temperature.

Dotted line- the normal curve; solid line- the expected curve of relationship between metabolism and temperature for fish previously adapted to each of the temperatures at which the metabolic rate is measured (see the text).

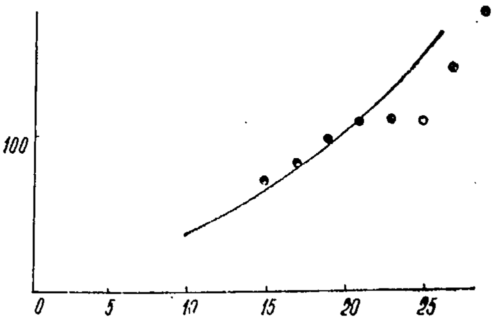

Fig. 16 [page 39]

Relationship between metabolic rate of carp and temperature, from data of Schmeing-Engberding (1953). Axes as in Fig. 2. See the text, page 38.

by so many factors that it is hardly possible to come to definite conclusions by merely studying "curve forms". More penetrating conclusions will become possible after it has been clarified how the metabolic level of fish changes in the course of acclimation to different temperature conditions.

3. Relation of the level of metabolism of fish to individual temperature acclimation

[page 40]

As long ago as 1936 I drew attention to the great general biological interest of the first published material which showed that acclimation to low temperatures is accompanied by an increase in metabolic rate, and that the reverse phenomenon is observed in the case of acclimation to high temperatures (Winberg, 1936). For fish, this phenomenon was pointed out by Wells (1935a, 1935b). He discovered, for Fundulus parvipinnis, that the metabolic rate of fish which had been acclimated to 20-24° was about 30-40% lower than in fish acclimated to 10-12°, when measured either at 12° or at 20°. Similar results were obtained in two experiments with Gillichthys mirabilis. One group of these fish was kept at 33° for 17 days prior to the experiment, and the other group at 11° for 20 days. Both groups were tested at 20°. In the cold-adapted fish the level of metabolism was 30-40% higher than in the warm-adapted group. This difference was strictly maintained throughout the entire time of observation (50 hours).

With regard to these and similar experiments, it must be noticed that at different temperatures it is very difficult, as a practical matter, to ensure the uniformity of other conditions, so that it is easy to ascribe to the direct action of temperature effects which really stem from accompanying circumstances. For instance, the same volume of water at different temperatures is not at all sufficient to create a uniform gas regime. In order to achieve the latter, it is advisable to use larger vessels when the temperature is higher. Wells says that prior to his experiments the fish had been starved for 24 hours. However, equal periods of starvation at 11° and 33° are not at all equivalent physiologically. At 33° it takes 8 times more reserve substance and oxygen to meet the requirements of metabolism than at 11°. Such considerations call for caution in interpreting the data of some authors, mostly foreign, who have studied the influence of temperature acclimation and as a rule have underestimated the complexity of the phenomenon and the possibility of indirect effects of different temperature conditions (Winberg, 1937).

Precht (1951) published the results of measurements of the rate of oxygen consumption of eels that had been acclimated to 11° and 26°. The flowing water method was used. In stating his results Precht, who appears to be entirely unfamiliar with the work of other authors using this method, has a lot to say about the increased rate of oxygen consumption that he discovered, apparently unaware that this is a common and well-known phenomenon (see page 17). The basic condition for successful use of the method, [page 41] that measurements must not begin until after a constant level of metabolism is established, was not observed in Precht's experiments. Furthermore, the eels, in order to eliminate motion, were narcotized with urethane. All this, as well as his confused presentation, makes it practically impossible to use Precht's data. Nevertheless, from the results of all the experiments as summarized in figure 8 of the work quoted, it can be seen that eels acclimated to 11° apparently had a higher level of metabolism at all temperatures (10-27°) than did eels acclimated to 26°. On the other hand, eels acclimated to 26° exhibited such a low rate of oxygen consumption (especially at 10°) that it seems very doubtful whether this is really due to the influence of the temperature at which they were held prior to the experiment, and not some other accessory causes not taken into consideration.

No such doubts arise concerning the work of A. P. Shcherbakov (1937), which is above reproach as regards methodology. For this reason this work is of special importance to an understanding of changes in metabolic rates of fish under the sustained influence of different temperatures. For his study of this problem Shcherbakov used a species which is extremely well suited to the purpose, namely the river lamprey (Lampetra fluviatilis). An adult river lamprey doesn't feed. During the experiment many lampreys attached themselves by suction to the walls of the respirometer and remained completely motionless. Using the flowing water method, Shcherbakov showed that shortly after the lampreys had been placed in the respirometer a constant rate of oxygen consumption was established, and was maintained indefinitely. All measurements of oxygen consumption were made at a temperature of 15.5-17.5°. Prior to the measurements the lampreys were kept at 3 different temperatures for a considerable length of time: 1.5-3.5°, 7-9° and 15-17°. The rate of oxygen consumption of the lampreys of the first group (average of 7 measurements) was 0.21 mg O_2 per gram per hour; there was little variation in the results of separate measurements (0.20-0.24). For 7 experiments with the second group of lampreys it amounted to 0.17 mg O_2/g/hour (range 0.15-0.19). For 12 measurements with the third group of lampreys it amounted to 0.14 mg O_2/g/hour (0.12-0.16). Hence in this case too the metabolic rate of specimens acclimated to a low temperature (about 2°) was higher, by 23%, than that of lampreys acclimated to 8°, and was 50% higher than lampreys acclimated to 16°. Shcherbakov's data are important evidence in support of the view that in fish and, so it seems, many other poikilothermous animals as well, adaptation to high temperatures is accompanied by reduction of metabolic level, whereas adaptation to low temperature is accompanied by increase in metabolic level.

Precht (1949) supports the existence of such a general law, on the basis of his own and published work, particularly that of N. S. Stroganov and A. P. Shcherbakov, [page 42] and even makes an attempt to distinguish several types of changes in metabolic rate in acclimating to different temperatures. This attempt deserves little attention because inadequate experimental data make it mainly speculative. Moreover he states the problem in a confusing and superficial manner. Precht assumes that in one and the same organism the type of temperature adaptation of metabolism can differ at different seasons. To me it seems that not the type, but only the outward manifestations of adaptation can differ at different times in the same animal. Better founded and more interesting is Precht's statement that a change in level of metabolism during acclimation does not occur in all organisms, but only in eurythermal ones, which in their natural environment encounter great temperature fluctuations. From this point of view the changes in the metabolic level during acclimation to temperature are not of a fundamental [vseobshchiĭ] character, rather they have been evolved as an adaptation. Some important data of other authors support this view. It has been shown that, of two species of littoral crustaceans, in the one (Emerita talpoida) which retains its activity during winter the metabolic rate rises as a result of the acclimation to low temperatures, whereas this does not occur in Talorchestia megalophthalma which is inactive in winter.

In the same laboratory, and using a good method (the manometric respirometer of Scholander), the respiration of the fish Tautogolabrus adspersus was measured at a temperature of 15°, both in summer when the fish in their natural environment live at temperatures of 18-22° and also in the winter when they live at 1-2°. A considerable number of measurements, made at various temperatures from 1° to 30° (Fig. 10), disclosed only a slight increase in the metabolic rate in winter. The smallness of the change in metabolic level with acclimation temperature in the case of Tautogolabrus is explained by the writers as a result of the fact that in winter these salt-water fish abandon the coastal zone and lead an inactive life. If this supposition is correct, then one must not expect great changes, on acclimation to high or low temperatures, for all the organisms which can survive considerable temperature fluctuations, but only for those which lead an active life over a wide temperature range (Edwards, 1943, J. cell. comp. Physiology, 21).

Freeman (1950) measured the tissue respiration of the muscles and of brei from the brain of goldfish which had been previously acclimated to different temperatures. He maintains, but without providing any numerical data, that the rates of oxygen consumption of the muscles of fish adapted to 12° and to 27° did not differ. This makes it impossible to directly associate [page 43] changes in metabolic level, in the process of acclimation, with any corresponding change in the tissue metabolism of the muscles. In contrast to muscle respiration, the rate of respiration of the brain tissue, which was measured at 18.9°, exhibited a well-developed inverse relation to the temperature the fish had been acclimated to. It was also shown that changes in metabolic level in acclimation were accompanied by corresponding changes in the frequency of respiratory movements. From this Freeman believes that the metabolic activity of the brain is the main factor determining the level of oxygen consumption of fish. Figure 17 shows the speed with which the changes occur that characterize the acclimation to 12° of fish which previously had lived at 27°. This drawing gives data for the rate of oxygen consumption rate of the whole fish and for the brain tissue, and also the frequency of the breathing movements at various times after the fish had been placed in the low temperature. In this case the acclimation is completed, in the main, during the first 48 hours. In practice, research workers who wish to obtain fish fully acclimated to a particular temperature usually consider it necessary to keep the fish at this temperature for several days at least, and in most cases for two weeks or more.

Although it has not yet been adequately shown how metabolic level changes during temperature acclimation, there are nevertheless [page 44] several serious experiments which support the view that, at least in many cases, the acclimation of fish to low temperatures is accompanied by an increase in level of metabolism, and that the reverse occurs on acclimation to high temperatures. If this phenomenon is actually widespread and sufficiently pronounced, the inevitable consequences must be: 1) a higher metabolic rate among fish which live at the lower temperatures under natural conditions, 2) a greater metabolic rate among fish in winter, 3) the existence of "adaptation zones", or flattened portions of the curve relating metabolic rate to temperature, for fish that are acclimated to each of the experimental temperatures, as compared with the corresponding curve obtained from short applications of different temperatures.

Let us now consider, as far as is possible at present, to what extent these phenomena actually occur. In order to answer the first question one should compare the level of metabolism of a number of specimens of one species, or even of one population, living under different temperature conditions. Among data familiar to me, those of Sumner come closest to meeting these conditions. Sumner and Lanham (1942) studied the rate of oxygen consumption of the fish <u>Grenichtys baileyi</u> (Gilb.), which inhabits a hot spring (37°). Contrary to the

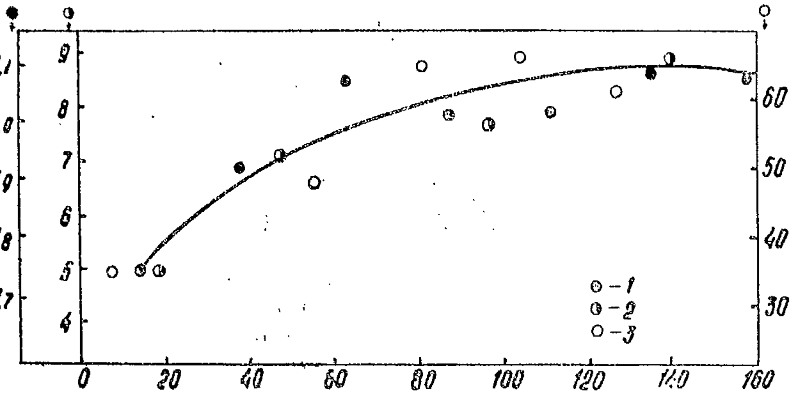

Fig. 17 [page 43]

The influence of temperature acclimation on metabolic rate and number of respiratory movements of goldfish, from Freeman's (1950) data.

Abscissa--time in hours after the fish had been carried from water at a high temperature (27°) to water at 12°. Ordinate--O_2 consumption in mg/kg/min (1); consumption of oxygen by brain tissue, in the same unit (2); number of respiratory movements per minute (3).

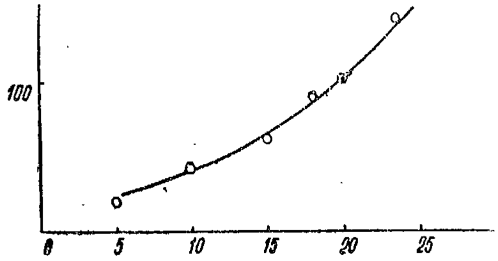

Fig. 18 [page 46]

Relation between metabolic rate of the American Salvelinus fontinalis and temperature, from Graham's (1949) data. These data were obtained from fish that had been acclimated beforehand to each of the temperatures at which oxygen consumption was measured. Axes as in Fig. 2.

original expectation of the authors, fish of the population which lives in a hot spring in Nevada (U.S.A.), at a temperature of 37°, showed the same rate of oxygen consumption after being placed in a reservoir containing water of 21°, as did fish of the same species which had always lived in that reservoir. Although the authors encountered some difficulties with regard to methods, they performed a great number of experiments, and a careful study of them leads to the conviction that the conclusion to which they came is well enough founded, even though it contradicts the results of laboratory experiments. However, it must be said that the fish from the populations inhabiting the hot and the cold bodies of water differed somewhat in meristic features.

On the basis of published data, it is difficult to say anything definite regarding seasonal differences in the metabolic rate of fish. Only isolated references to this subject are found in various papers. For example, A. O. Tauson mentions that "fish caught in the Kama River in early spring when the river temperature is low (5-6°), if used in experiments (at 15-16°), yield high values for the rate of oxygen consumption in comparison with fish caught in summer". It is difficult to know how well founded this statement may be. Furthermore, it is clear that under natural conditions seasonal differences in metabolic rate may be associated not only with temperature but also with different conditions of feeding, respiration, and so on.

[page 45] The work of G. N. Bogdanov and S. V. Streltsova (1953) contains some very peculiar information concerning seasonal differences in fish respiration. These authors measured the rate of oxygen consumption of several species of fish from Lake Ilmen, in summer and in winter. The method used in their research unfortunately was not stated but the context makes it clear that the sealed vessel method was used. In winter the fish were kept in ponds at a very low temperature (0.2°) prior to the experiments. The peculiarity of the data obtained consists in the fact that, judging by the figures quoted, in winter there was very little change in metabolism with change in temperature. It is easy to see that within the range of 0° to 10° the temperature coefficient (Q_{10}) was 1.36 for pike, 1.46 for perch, 1.55 for roach, and 1.32 for ruffe. Comparing measurements made in March and in July at 10°, we see that in every case the metabolic rate was higher in July, namely: for bream 29.9 and 64.0 mg O_2 per kg of weight per hour, respectively; for zander, 35.8 and 77.3; for pike, 49.8 and 68.7; and for perch, 47.4 and 93.4. Such a result is unexpected in view of the data, given above, which indicate a lowering of the level of metabolism with acclimation to high temperatures. However, there is good reason to regard this material with caution. For example, the tables contain the results of measurements of the rate of oxygen consumption of fish of different sizes. In many cases (Table 7 and others)

the metabolic rate increases as the weight of the fish increases, instead of decreasing, which is quite unexpected. The authors pay no attention to the peculiarity of their data, they consider it unnecessary to describe the conditions under which they were obtained, and they quote unbelievable values for respiration coefficients without any comment (page 8), so that it is difficult to avoid thinking that unconsidered methodological errors may be involved.

Of special interest for our purpose is the course of the curves describing the relation of metabolic rate to temperature for fish that had been acclimated beforehand to each of the temperatures studied. Freeman (1950) gives in graphical form the results of measurements of the rate of oxygen consumption of goldfish at 4 acclimation temperatures (12°, 20°, 27° and 37.8°). He plotted a curve representing the mean values of a few widely divergent observations. According to this curve the oxygen consumption was about 1.8 mg O_2 per kilogram per minute at a temperature of 12°; it was 2.4 at 20°, 3.5 at 27°, and at 37.8° it was only about 1.1. Our attention is drawn to the small difference in the metabolic rate at 12° and 20° and, particularly, to the exceptionally low metabolic rate of the fish kept at such a high temperature as 37.8°. In the latter case there can be no doubt that the metabolism of the few fish that survived such extreme conditions [page 46] was greatly lowered for other reasons besides the acclimation. Apparently no great significance should be attached to these data of Freeman's, for in the carefully conducted work of Fry and Hart (1948), who have great experience in the quantitative study of fish metabolism and the process of acclimation, altogether different results were obtained for the same species. In particular, it was not found that the metabolic rate at 35° was any less than at lower temperatures. The authors of this valuable study accepted the length of time necessary to attain stability in respect to lethal temperature as the period necessary to acquire complete [temperature] acclimation. At a temperature of 5° it required 20 days, but at 35° it required only 4 days.

The authors draw special attention to the fact that their data, which were obtained following complete preliminary acclimation of the goldfish to each of the temperatures studied, agree beautifully with Krogh's data that were used for the construction of the "normal curve", and also with the results of the metabolism measurements of goldfish made by Gaarder and his colleagues (1922, fig. 11).

In the same laboratory, and with the same high standard of laboratory technique, Graham (1949) carried out her research using fingerlings of the American char Salvelinus fontinalis. In this case, also, the fish used in the experiments were kept for a long time (weeks) at the respective temperatures before making the measurements, so that full temperature acclimation would be obtained. The data obtained for standard metabolism are shown in Fig. 18, which shows how closely they follow the normal curve. In comparing these data with the analogous data of Fry, obtained from goldfish, important conclusions emerge. First of all, as Graham herself states, there is no confirmation of the opinion expressed earlier by Fry, that at moderate temperatures the metabolic rate of cold-water fishes is more affected by temperature than is the metabolism of warm-water fishes. Further, neither for the char nor the goldfish were there any indications of "flattened [page 47] sectors" of the curve. Most important of all is the fact that under conditions of complete temperature acclimation the normal curve, which was originally obtained for relatively short applications of temperature, is quite suitable for describing the standard metabolism of both these species: the warmth-loving goldfish whose upper lethal limit is 37°, and Salvelinus with a lethal limit of 25°. It is not easy to reconcile this fact with the evidence that there is a decline in the level of metabolism of fish when acclimated to high temperatures and an increase when they are acclimated to low temperatures. As noticed earlier, a necessary consequence of this phenomenon would have to be a more [gently] sloping curve relating rate of metabolism to temperature when there is a sustained application of the various temperatures. However, this was not confirmed by the experiments of Fry and Hart (1948) and Graham (1949). Nevertheless, it is very hard to abandon what seemed to be a well-founded conclusion--that a rise in metabolic level occurred with acclimation to low temperatures, and the reverse for high ones. We have here a case of a plain contradiction in the stated results of carefully conducted experimental work.

Although it is not at all clear how this contradiction will be resolved in the future, the data of this most recent work show convincingly that, as a first approximation, the "normal curve" describes the relation of metabolic rate to temperature sufficiently well not only when the change is rapid, but also when there is a sustained application of each temperature studied. It is hard to overvalue this fact, which greatly enhances the usefulness of the relationship expressed by the normal curve and broadens the scope of its applicability. In particular, it makes us more confident that under natural conditions the relation of fish metabolic rate to temperature can be expressed by the "normal curve" with sufficient accuracy. The data of Winberg and Khartova (1953), obtained by measuring the rate of oxygen consumption of carp fry and fingerlings caught out [of a pond] just prior to the experiment, are of some interest in this connexion (all measurements were made at the temperature of the water of the pond, the jar being submerged into the pond water for the duration of the experiment). The data obtained, taking into consideration the inevitable scatter in the results of individual measurements made at different times on fish of different sizes, show that under natural conditions the relation of the metabolism of fish to temperature is close to that expected according to the "normal curve".

Nevertheless, in spite of this it cannot be maintained that the average metabolic rate of fish under natural conditions is always accurately expressed by the "normal curve". It is necessary to bear in mind that all the data mentioned above were obtained under laboratory conditions, when motionless or slowly moving [page 48] fish were used. Data concerning the relation between fish metabolism and temperature during "intensive motion" are given below (page 171).

4. The relation of the metabolic level of fish to the temperature adaptation of the species

What has been stated hitherto concerns either the immediate influence of temperature upon the metabolic rate of fish, or the consequences of individual adaptation [acclimation] to different temperature conditions. We must consider separately the effect of temperature on the metabolism of fish from the point of view of their adaptation as a species, i.e. the constitutional peculiarities which reflect the environmental conditions under which they were formed during the process of evolution. Data which shed light on this question are still very scarce. We may recall the attempt by Schlieper (1950, 1952) to show that in stenothermal cold-loving animals, fish in particular, the metabolic rate is more dependent on temperature than in eurythermal organisms. This author (1950) even considers it possible to affirm that the "relative thermostability" of eurythermal species is so great that their metabolic rates can be the same at temperatures which differ by 10°. However, these controversial statements are not sufficiently supported by convincing numerical data. In the 1952 work, without stating the method of measurement or other necessary information, the data are given in the form of a graph of individual measurements of the rate of oxygen consumption of Squalus cephalus and Trutta iridea[1], made at only 3 temperatures. In this work material is presented which, in the author's opinion, proves that the nature of the relation of metabolic rate to temperature is affected by the ionic composition of the environment, possibly by influencing the "degree of the hydration" of the tissues--a pet idea of Schlieper's. Schlieper's views cannot be accepted, both because they are crudely mechanistic and speculative in nature

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[1] Here and elsewhere the scientific names are those given by the original authors.

and because they are "confirmed" only by primitive and carelessly described experimental data. It is noteworthy that Schlieper's ideas are only slightly reflected in a recent work of his students (Floerke, Keiz and Wangorsch, 1954). It can easily be seen that the data they obtain (tables 7, 17, 18, 24, 26) for the metabolic rate of various fishes (trout, chub, gudgeon, roach) at different temperatures follow the normal curve beautifully. There is no mention either of depressed sectors of the curves, or of the data of Schmeing-Engberding.

[page 49] For an understanding of the nature of the adaptation of species to different temperatures in their normal habitats, the investigations of Scholander and his colleagues (1953) are of very great importance. This research was carried out by workers in a laboratory that is specially engaged in studying the metabolic rates of different members of the aquatic fauna. Metabolic rates of various representatives of the animal kingdom, fish among them, were studied in the tropics (Panamá) and under arctic conditions (Alaska). In all, 4 species of tropical fish and 7 species of arctic fish were studied. It was established that the lower temperature limit at which fish begin to die is very high for tropical fishes--15-20°. The upper limits also differ radically. Arctic fishes which inhabit water with temperatures close to 0° die at 10-20°, whereas tropical fishes die only when temperatures reach 35-40°. Thus the biokinetic temperature ranges of tropical and arctic fishes scarcely overlap, and a comparison of their metabolic rates at the same temperature is practically impossible. The metabolic rates of representatives of both groups were studied at temperatures which embrace the entire range of their respective biokinetic temperatures. Values of temperature coefficients, which were very close to those anticipated from the normal curve, were calculated from the data obtained. The authors emphasize especially that no characteristic differences were discovered between values of the temperature coefficients for arctic and tropical fishes. In other words, a conclusion stated in an earlier work by Peiss and Field (1950), carried out in the same laboratory, was not confirmed. In Alaska the latter authors measured the metabolic rate of brain and liver tissue of the arctic fish <u>Boreogadus saida</u> at various temperatures, while in a California laboratory the golden orfe (<u>Idus melanotus</u>) was used. It was found that the tissue respiration of the arctic fish was distinguished by one peculiarity, namely that it did not exhibit the usual increase of the temperature coefficient at low temperatures. But the tissue respiration of the brain and liver of the golden orfe corresponded very well with the normal curve. Peiss and Field ascribed a general significance to this difference. They interpreted the constancy of the temperature coefficients in the case of the arctic fish as an adaptation enabling the fish to maintain a relatively high metabolic level at low temperatures. It must be said that although Scholander <u>et al</u>. dispute this conclusion of Peiss

and Field, in their own data a constancy of temperature coefficients at low temperatures is exhibited by three of the four species of arctic fish that they studied. It appears that the possibility of such an adaptation to low temperatures must still be considered (Rao and Bullock, 1954).

[page 50] The relation of the metabolic rate to temperature in the case of tropical species of fish follows the normal curve well, according to Scholander's data.

The most interesting result is a comparison of the metabolic levels of tropical and arctic fish. The metabolic rate of tropical fish, measured at a temperature close to that of the water in their natural habitats (30°), was only 3-4 times greater than the metabolic rate of arctic fish measured at a temperature of 0°. Hence the authors conclude that arctic species have a high metabolic level (Fig. 19). In other words, the study of the adaptation of species has yielded the same result as did the study of the acclimation of individuals.

The great bulk of published data on the metabolic rate of fish has been obtained from marine and freshwater species in the temperate zone. Therefore, the generalization from the available material on metabolic rate of different fish, given below, refers to fish of temperate latitudes; these are the fish from which the "normal curve" relating basal metabolism to temperature was experimentally determined, and hence it is to them, primarily, that it should be applied.

* * *

In summary, we may conclude that the general character of the relation between basal metabolic rate and temperature, for fish of different systematic positions, ages, and sizes, can be expressed with sufficient accuracy for practical purposes by the "normal curve". This relationship was obtained empirically and has been confirmed [page 51] by a large amount of material.

Much less is known about the causes which determine the precise character of the relationship between basal metabolic rate and temperature, for a particular species and in a particular set of environmental conditions. There are many reasons to believe that, among the factors that influence metabolic level, an important role is to be ascribed to temperature adaptation. However, in view of discrepancies which still persist in the experimental data concerning this problem, it is difficult to appraise the significance of this phenomenon under natural conditions. Almost all the data at hand concerning the relation of fish metabolic rate to temperature were obtained from motionless or slowly moving fish. In order to form an opinion about the metabolic rate of fish under natural conditions it is especially important to know how temperature influences the metabolism of fish during activity. For this reason the clarification of this aspect of the problem is the most important task of further research in this field.

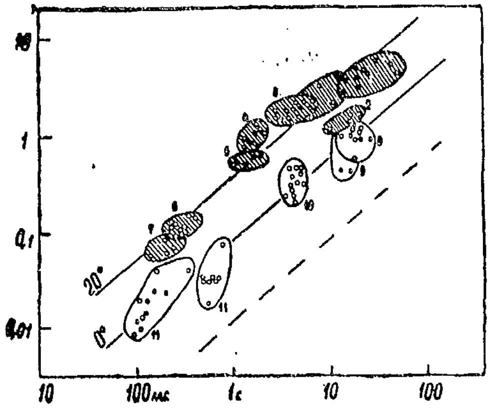

Fig. 19 [page 50]

The metabolic level of tropical and arctic fishes, according to measurements by Scholander _et al_. (1953).

Abscissa--weight of the fish; ordinate--oxygen consumption in ml per specimen per hour at the temperature indicated. The dotted line is the calculated metabolic level of tropical fish at a temperature of 0° (see the text, page 50).

Chapter III. [page 52]

The Relation between Metabolic Rate of Fish and the Degree of Saturation of the Water with Oxygen

1. The general character of the relation of metabolism to oxygen content of the water

Fish, as well as all other aquatic animals, under natural conditions encounter various oxygen contents in the water--from the not uncommon cases where dissolved oxygen is lacking altogether, to situations where the water is supersaturated with this gas, as frequently occurs as a result of the photosynthetic activity of aquatic plants. In order to be in a position to judge to what extent this factor can influence the results of the measurements of the rate of oxygen consumption, it is necessary to know how the metabolic rate of fish is related to the oxygen content of the environment. Since the time that Winterstein (1908) and Henze (1910) published their data indicating that rate of oxygen consumption is independent of partial pressure of oxygen in the environment, the question for a long time remained unsettled, because while there was no shortage of data supporting Henze's and Winterstein's view (Gaarder, 1918; Amberson *et al.*, 1924; Keys, 1930a), neither was there any scarcity of data which contradicted them.

It is now quite clear that it is wrong to state the problem in the form of whether the metabolic rate does or does not depend on partial pressure of oxygen in the environment. Rather, it must first be made clear what range of oxygen concentrations, and what species, are involved in each case. Without dwelling on every stage in its development, we will describe the present state of knowledge in this field by giving examples of recent research.

Lindroth (1941, 1942), using an original method (page 12), measured the rate of oxygen consumption of roach, salmon and pike, and also that of the developing ova of salmon and pike, at various dissolved oxygen contents. Lindroth believes that as long as the oxygen content of the water is sufficiently high the rate of oxygen consumption will remain constant, among all the fish he studied. It becomes reduced if the oxygen content in the environment drops below a certain [page 53] "critical point" [kriticheskaîa tochka]. According to Lindroth, the lower the temperature, the lower is the oxygen content at the critical point. Lindroth's graphs show, for example, that at 23° the critical oxygen content for roach is close to 45% saturation. In the case of salmon at 20° it is close to 33% of saturation. At 7° the critical point for roach is reduced to 10% or 11% of saturation, and for salmon at 9° it is close to 20%.

T. I. Privolnev (1947) made many observations on the oxygen consumption rate of various fishes at different environmental oxygen contents and at different temperatures. It is advisable to study the results of this important research after we have obtained a definite idea of the nature of the relation of fish metabolism to the partial pressure of oxygen in the environment from the information in several recent publications.

The nature of the relation between metabolic rate of fish and rate of oxygen consumption is especially well exemplified by the excellent work of A. B. Lozinov (1950, 1952, 1953). This author studied the relation of the rate of oxygen consumption to the oxygen content of the environment for fry and fingerling sevriuga and osëtr, for perch fingerlings, and for yearling perch and tench. He used a modified sealed-vessel method in a form that would permit drawing samples of water to determine the oxygen content during the experiment. The oxygen content in the water was reduced by the respiration of the fish. Because of the ample size of the respirometer each experiment was continued for 12-14 hours. By this method many observations were made, which are shown by means of curves relating the rate of oxygen consumption to the oxygen content in the water. Lozinov regards the curve shown in Fig. 20 as a typical one. Considering the curve from <u>right to left</u>, we notice first the portion (indicated by the fine dotted line) which, according to Lozinov, corresponds to the increase in oxygen consumption [<u>page 54</u>] by the fish during the first little while after they are placed in the respirometer. In other words, the initial decline in the curve is not related to the small reduction of the oxygen content at that time. We shall see below that this rather important circumstance has not been taken into consideration by a number of authors who have used the sealed vessel method. Next, there is a horizontal sector of the curve, which corresponds to those concentrations of dissolved oxygen at which the metabolic rate remains at a constant level. Lozinov, following Privolnev, calls this sector the "oxygen zone of adaptation" [kislorodnaía zona adaptatsii]. After a certain environmental oxygen content is reached--the "critical concentration" [kriticheskaía kontsentratsiía]--the rate of oxygen consumption decreases, and this continues until the threshold [porogovaía] concentration is reached. At this latter stage not only is the metabolic rate sharply reduced, but the fish begin to die. It is a good idea to adopt the terminology employed by Lozinov, and used in the later works of Privolnev, i.e. to differentiate strictly between the critical concentration and the threshold concentration. Up to not so long ago the threshold

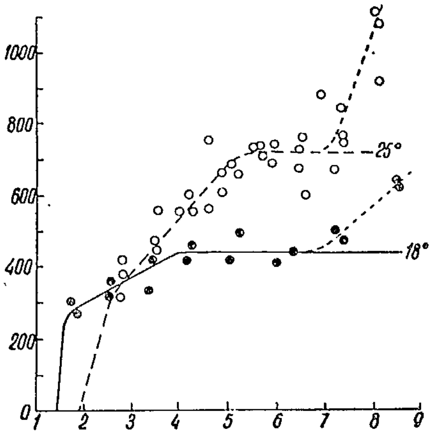

Fig. 20 [page 53]

Relation between the metabolic rate of sevriuga fingerlings and the oxygen content of the water at temperatures of 18° and 25°.

Abscissa--oxygen content of the water in mg/l; ordinate--rate of oxygen consumption in mg/kg/hour. (After Lozinov, 1952).

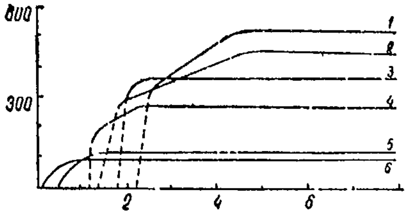

Fig. 21 [page 54]

Relation of the metabolic rate of various freshwater fishes to the oxygen content of the environment, from data of A. B. Lozinov (1950).

Ordinate--oxygen content of the water in mg/l; abscissa--oxygen consumption in mg/kg/hour. 1- fry of sevriuga at 18°; 2- fingerling sevriuga at 18°; 3- fingerling osetr at 18°; 5- perch at 11°; 6- tench at 11° (from a Dissertation, 1950).

concentration had been called critical concentration (Privolnev, 1947). Unfortunately some authors have confused these terms very recently. For instance, the heading of table 4 in N. D. Nikiforov's work mentions "critical oxygen tensions" whereas in the text the same values are designated as "threshold" tensions.

The relation of the critical oxygen content to temperature is clearly evident in Lozinov's data (Fig. 21). The higher the temperature, the greater is the oxygen content in the environment at the turning point. In other words, the higher the metabolic level, the greater is the oxygen content in the environment at the point where a reduction in oxygen consumption sets in. The metabolic level is of prime importance for the position of the critical point, as shown by the data for various species in Fig. 21.

Thanks to the fact that at higher temperatures metabolism proceeds at a faster rate, the critical oxygen content [page 55] (i.e. the point where the bend in the curve begins [going from right to left]) shifts to the right and the horizontal sector of the curve is reduced accordingly. Therefore, from data obtained at a high temperature, as Lozinov aptly remarks, "it is difficult to tell where the reduction of the respiration rate following the period of accelerated respiration of the young fish at the beginning of the experiment ends, and where the actual inhibition of respiration due to shortage of oxygen begins". Such conditions can easily lead to a wrong conclusion, namely, that a slight reduction in the oxygen content in the environment reduces the metabolic rate.

When studying the curves obtained by Lozinov, it is easily seen that in some cases the two turning points of the curve (the critical and threshold oxygen contents) and the sloping sector of the curve between them, are not sufficiently well indicated. Frequently, especially at low temperatures, the critical point can be close to the lethal oxygen limit (the oxygen threshold). The apparent cause of this difference lies in the fact that in using Lozinov's method the fish, and especially the small fish, were able to swim about in the rather large respirometer used. Hence, actually, it was not the basal or standard metabolism that was being measured, but a somewhat larger value, the metabolism when the fish were in motion (the active metabolism). It is quite possible, in the cases where the sloping sector of the curve between the critical and threshold concentrations is well developed, that the reduction in rate of oxygen consumption after the critical content has been reached occurs as a result of suppressing the activity of fish under these conditions. In fact, Lozinov remarks that the "inhibition of respiration is accompanied by oxygen-starvation of the young fish, which is reflected particularly in a rapid reduction of their mobility". It is only necessary to make a plausible assumption, namely that at low temperatures the mobility of the fish was less, in order to understand all the peculiarities of the data obtained by Lozinov. We may note that many authors studying the relation of metabolic rate to partial oxygen pressure in the environment have used motionless fish and the flowing water method, and have obtained curves with only one flexure.

The difference between data obtained from motionless fish and those from fish that are in active motion was demonstrated by the important researches of Fry (1948) and Graham (1949). By means of a special annular vessel, which rotates on bearings, Fry brought about conditions under which the fish (goldfish) were compelled to swim at a definite speed. By changing the speed of the vessel Fry was able to observe how the metabolic rate changes in relation to the speed at which the fish is moving. These data of Fry's are treated in detail below (Chapter IX). The same device enabled Graham (1949), in the same laboratory, to study [page 56] how metabolic rate depends upon the oxygen content in the water when a fish moves at its maximum speed. Fingerlings of Salvelinus fontinalis were used for the experiments, having an average individual weight of 27 grams (Fig. 22, 23). Graham defined the minimal metabolic rate for a 24-hour period as the standard metabolism. In these experiments, as is usual, the level of standard metabolism increased uninterruptedly with increase in temperature. In contrast to this, the metabolism during the height of activity increased only up to a certain maximum, which was attained at a temperature of about 20°. As the temperature continued to rise beyond that point, the metabolic rate decreased again. It is especially important that, according to these data, the metabolic level depends upon temperature only if the oxygen content in the environment is sufficiently high. If the oxygen content in the water is below the critical concentration, then this factor [oxygen] is of decisive importance, and temperature then has only a very slight effect on metabolic level. In the range of ordinary temperatures (13-24.5°), when the oxygen content is insufficient the metabolic rate is very similar at all temperatures, and depends only on the partial oxygen pressure of the medium. These data show clearly that [page 57] the position of the critical point is wholly determined by the height at which the horizontal sector of the curve is located, i.e. by the level of metabolism when there is adequate ambient oxygen; which level, in turn, depends on the temperature and on the degree of activity of the fish.

This leads to important conclusions. First of all, it is clear that in describing the relation of any fish to oxygen conditions, there is no sense in stating the position of the critical point without referring to the metabolic level. Whenever the position of the critical point is indicated it must be stated at what metabolic level it was determined.

The different positions of the critical points at

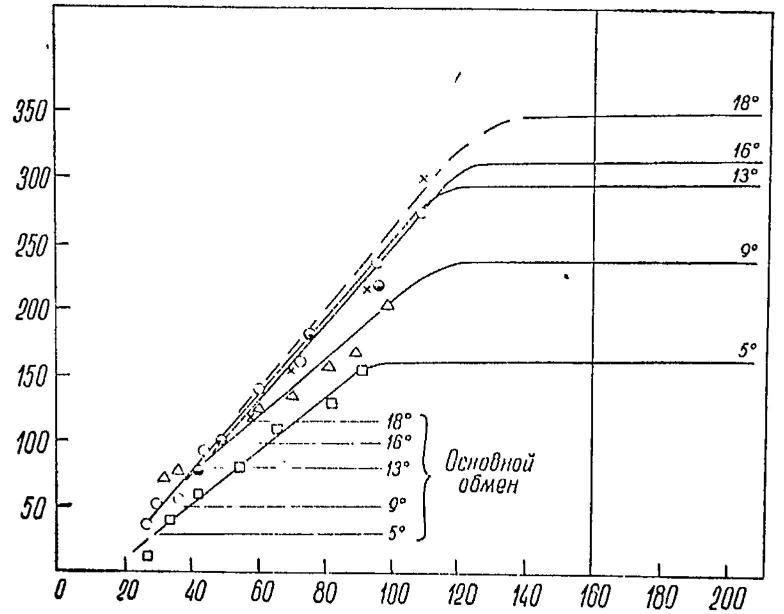

Fig. 22 [page 56]

Relation between the active metabolic rate of the American Salvelinus fontinalis and the oxygen content of the environment, at various temperatures.

Abscissa--partial pressure of O_2 in mm Hg; ordinate--consumption of O_2, in ml/kg/hour. The metabolic level in a state of rest is also shown (Graham, 1949).

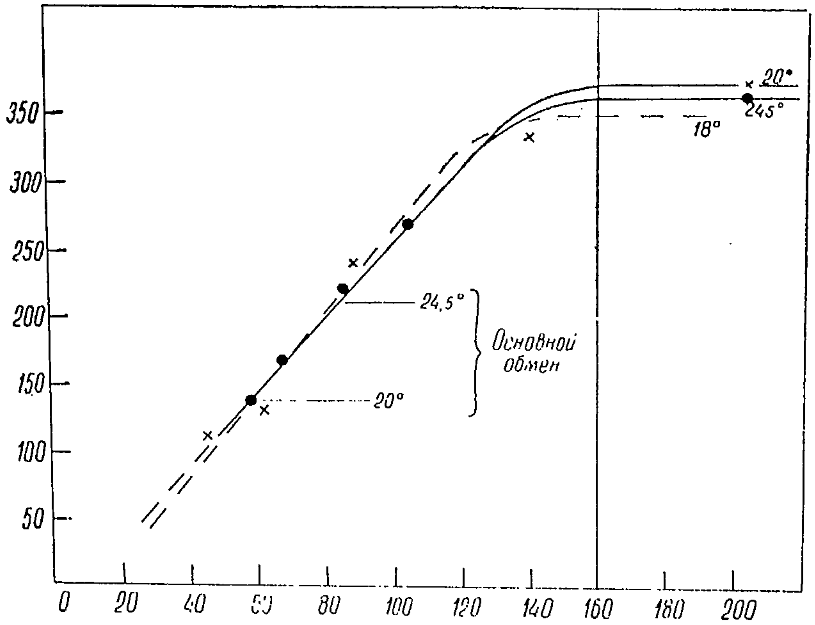

Fig. 23 [page 57]

The same as Fig. 22, but for 20° and 24.5°.

different metabolic levels does not, however, indicate a different relation of the subjects to oxygen conditions. The metabolic level need only be lowered, perhaps only as a result of a decrease in activity, in order to reduce the critical oxygen tension also. In keeping with this, as is clear from Fig. 22 and 23, the segment of the sloping curve which lies between the critical point for metabolism at maximum activity and the critical point for basal metabolism, corresponds to the oxygen zone over which only restricted activity is possible; and this was actually established by Graham.

[page 58] A valid comparison of the critical points for different species can only be made when they are compared at the same metabolic level. For any other cases, one must know how the position of the critical point is related to the metabolic level for each subject under the conditions actually prevailing.

How important it is to take this circumstance into account can be seen from the data of Nikiforov (1953, table 1). These data were obtained while studying the oxygen consumption rate of young salmon, and I have plotted them in Fig. 24. It is clear from the figure that in this case too the close relationship between the respiration of the smallest fry and the oxygen content of the water occurs simply because they have an inherently high metabolic rate. There is no reason for saying, as both Nikiforov and Privolnev seem inclined to do, that, in addition to their different metabolic rates, young fish of different sizes and ages also differ in respect to their response to oxygen conditions. Of the same nature are Privolnev's data obtained from young roach of various ages (fig. 3, page 75), which show very clearly the relation of the critical point to the metabolic level. According to Nikiforov, among some salmon fingerlings raised in a pond with water of low oxygen content, "the critical oxygen tension was reduced and the respiration rate was lowered". Actually it should not be said that two effects were observed, but merely that there was a reduction in the respiration rate which inevitably also entails a reduction in the critical oxygen content. This can be seen from Fig. 24.

The above concept of the relation of the position of the critical point to the respiration rate provides a method by which the results of different observations may be generalized. For instance, G. N. Bogdanov and S. V. Streltsova (1953) measured the rate of oxygen consumption of bream, zander and perch at various ambient oxygen contents. In interpreting [page 59] their data, the authors conclude that they have discovered in their material differences in the nature of the relation of metabolic rate to the oxygen content of the water. Probably such differences do exist. However, if all the data of Bogdanov and Streltsova are presented in a graph, it is plain that there is no reason to assume that such differences were evident in this case. On the contrary, Fig. 25 shows convincingly that under the conditions of their experiments bream, zander and perch exhibited similar if not identical relationships to the ambient oxygen content, which fits nicely into the scheme described above. It is only this general result of the experiments conducted that deserves attention in this case, and not a comparison of the individual measurements, which are subject to considerable accidental fluctuation.

According to these experiments the maximum possible rate of oxygen consumption is directly related to the oxygen content of the water. For these conditions and materials, the position of the critical point in relation to metabolic rate can be determined approximately by the equation:
$x = 0.0227y + 0.454$, where: x is the critical oxygen content in mg/l, y is the oxygen consumption rate in mg/l per hour[1]. It is interesting to compare these data with the analogous material of Lozinov and Privolnev, shown in Fig. 21 and 24. In the two latter cases the critical points are attained at lower oxygen concentrations than in Bogdanov and Streltsova's report. For example, when the metabolic rate is 200 mg O_2/kg/hour, according to Bogdanov and Streltsova the critical point should be reached at an environmental O_2 content of approximately 5 mg/l, while according to Fig. 21 it would be 1.5 mg/l O_2, and according to Fig. 24, 3 mg/l O_2. It is evident that these differences must result from the conditions under which the measurements were made and the peculiarities of the material.

[page 60] Although the hypothesis just presented, that for any given material and environmental conditions the position of the critical concentration of oxygen is determined by the metabolic rate, often agrees well with the experimental data (Fig. 21, 24, 25), nevertheless no general significance need be ascribed to it. When metabolic levels have been shifted as a result of acclimation, there are parallel changes in the ability to utilize low concentrations of oxygen; with the result that the critical concentration of oxygen, when metabolic level is low, becomes even lower than would be expected as a result of the decrease in the metabolic level. The reverse situation is also possible, where a low metabolic level contributes to a decrease in ability to utilize low oxygen concentrations.

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[1] [This appears to be a misprint in the text. It would seem more likely to be mg/kg/hr.--F.E.J.F.]

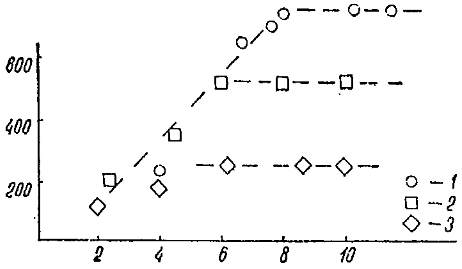

Fig. 24 [page 58]

Relation of metabolic rate of young salmon of various weights to the environmental oxygen concentration, according to Nikiforov (1953, table 1).

Abscissa--oxygen concentration in mg/l; ordinate--rate of oxygen consumption in mg/kg/hr at 14.5°. 1- fish of an average weight of 0.17 g; 2- fish of 1.25-2.6 g; 3- fish of 8.5-11.0 g.

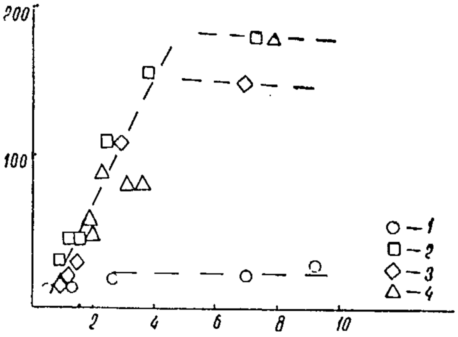

Fig. 25 [page 59]

Relation of metabolic rate of various fresh-water fishes to the oxygen content in the water, from data of Bogdanov and Streltsova (1953).

Abscissa--oxygen content of the water in mg/l. Ordinate--oxygen consumption in mg/kg/hour. 1- zander at 3°; 2- bream at 20°; 3- zander at 20°; 4- perch at 20°.

2. Some special aspects of the relation of fish metabolism to the oxygen content of the water

The concepts already discussed, concerning the general character of the relationship between metabolism and the environmental oxygen content, do not exhaust this complex subject, but they permit us to consider from a unified point of view the results of particular researches which have been interpreted in different ways. In this connection it will be appropriate to consider the basic point of view of Privolnev's (1947) work mentioned above, in which the sealed vessel method was used. Here, as in the experiments of Lozinov just described, the oxygen content in the water was reduced by the respiration of the fish used in the experiment, i.e. throughout the experiment the environmental oxygen content decreased continuously. The results of Privolnev's numerous measurements, which he presents only in the form of numerical data, disclose such an unusual scatter of the points when they are entered on a graph that they are not amenable to processing by objective methods and can be used only for the most general conclusions. The irregularity of Privolnev's material stems from the fact that the measurements for each species were made with fish of different weights and ages, while the weight of the fish used in each experiment is not mentioned. For example, table 21 contains data on the rate of oxygen consumption of pike. In the text it is only stated that pike "weighing from 0.08 to 0.45 g" were used in the experiment; further that "the respiration of some specimens was determined at a low oxygen content, that of others at a higher oxygen content". On page 94 we read that "a determination of respiration was made for an(?) ide, the weight of which varied from 0.31 to 1 kg".

In summarizing his data Privolnev writes: "For the 12 species of freshwater fishes studied, the relation of respiration to [page 61] the concentration of dissolved oxygen in the water is similar for all, in its general features. For all the fish studied, the oxygen consumption fluctuated independently of the oxygen concentration in the environment, within certain limits. A moderate degree of reduction of the oxygen content of the water causes some reduction in rate of respiration. A reduction of this amount is not lethal. A fish can live for a long time at such a level of metabolism. Further reduction in the oxygen content of the environment causes a serious reduction in respiration rate followed by death of the fish within a short time. The limits of the range of dissolved oxygen which cause reduced respiration and death differ for the different species of fish."

Furthermore, Privolnev believes that, in contrast to the respiration of "adult" fish, "in the early stages of the larval life a straight-line relation between oxidation processes and the partial pressure of oxygen can be observed. Afterwards this relationship gradually disappears. For most commercial fish this dependence of respiration upon the partial oxygen pressure decreases over a long period of time--up to 8-10 months after hatching". It is not altogether clear what materials this conclusion is based on. For example, from fig. 3 on his page 75 it can be seen that only when they were 10 to 15 days old did the fry of roach exhibit a direct relationship between respiration and environmental oxygen content. The next age-class (2-2.5 months) already exhibits a typical curve with a well-developed horizontal sector.

It is interesting that in another place this author indicates that stunted fingerlings (3 g) retained their "juvenile" type of relation of respiration to the O_2-content. From this one can conclude that size rather than age is what is of basic importance (Privolnev, 1953).

A. G. Mints (1952), who used the same method as Privolnev, fully shares his opinion that the respiration of fry is "directly dependent" on the oxygen content in the environment. However, her data, shown in a graph, reveal not a straight line but an ordinary convex curve.

In the light of the above it is plain that at the large rate of oxygen consumption characteristic of fry, the critical point must be shifted in the direction of higher oxygen concentrations, and the zone in which metabolism is independent of the partial pressure of oxygen is much narrowed. Under these conditions, when using the sealed-vessel method, the initial high level of oxygen consumption [due to excitement of the fish] can easily conceal the "zone of oxygen adaptation". This was not taken into consideration by Privolnev, who in his 1947 paper was inclined to take the view that any [page 62] reduction of metabolic rate observed in an experiment is to be explained by the reduction of the environmental oxygen tension, no matter how small the reduction may be. It is quite probable that the abovementioned differences between the respiration of fry and "adult" fish boil down to a matter of differences in metabolic level. If so, then there is no need to assume, as Privolnev does, that in fry the regulation of metabolic level by the nervous system "has not yet been established".

There are no grounds at all for regarding the constant respiration rate, which can be observed if the oxygen concentration in the environment is sufficiently high, as resulting from [nervous] regulation. There is no doubt of the great importance of regulation phenomena, especially when conditions approach the critical point. However, the presence of an oxygen zone within which metabolic level is constant is not in itself sufficient to warrant the association of this phenomenon of fish respiration (which is also found in tissue respiration and the respiration of bacteria, etc.) with the existence of nervous regulation of respiration. It should be said that even Privolnev does not always resort to this concept when he encounters a constant metabolic level. Thus, in regard to the respiration of ova during the period from fertilization to the time when the blood circulation is established, we read that "respiration takes place relatively independently of the partial oxygen pressure in the environment. There is no regulation of the respiration processes."

When studying data on respiration of the sterlet, Privolnev considers it possible to speak of "a graded [stupenchatoe] reduction of respiration when there is a reduction of the oxygen concentration" (Privolnev's fig. 4). Because he assumes that the very first reduction in the rate of oxygen consumption is associated with the reduction in the oxygen content in the environment, Privolnev is compelled to postulate that already at such a high oxygen concentration as 7 mg/l O_2 there occurs an "inhibition" of respiration in this species. If, following Lozinov, we take the view that the original reduction is not associated with partial oxygen pressure, then from these same data of Privolnev's we find that the critical oxygen content is at a considerably lower level, and is about 3.5 mg/l for the sterlet.

L. I. Markova (1949), who used the same method, observed that the peak of oxygen consumption in bream occurred during the first 15-30 minutes; after this the rate of respiration decreased. Afterwards, as she states: "as the experiment with the bream was continued and the partial pressure of oxygen was reduced to 80 mm Hg, the respiration rate of the bream was reduced [only] very slightly. But if the oxygen is reduced still more, the respiration rate of the bream again decreases." Thus in this case too an initial lowering of the metabolic rate was observed which the author quite erroneously attributed [page 63] to an effect of the partial oxygen pressure; then there followed a zone of independence of metabolism from [control of] oxygen content and, finally, below 80 mm Hg oxygen pressure the true critical point was located. One must assume that Privolnev (1947), Markova and several other investigators who have used the sealed-vessel method, have in many cases accepted as the start of the reduction of metabolic rate not the actual position of the critical point, but a different and larger value of the environmental oxygen content, which occurred in their experiments during the initial reduction of the rate of oxygen consumption. The difference between the value obtained in this way and the true critical point should be larger for active and excitable fish, and smaller for those less active and hard to stimulate. Privolnev provides table 2 as a summary of the results of his research. There is no doubt that this table, although based on a great deal of experience in the study of the metabolism of freshwater fish, for the most part shows accurately only the <u>relative</u> sensitivity of fish to an oxygen deficit in the environment, because the figures indicating the position of critical boundaries of oxygen content cannot be regarded as sufficiently well established for the reasons mentioned above; and for some fish at least they must be exaggerated.

It must be remembered that the more exact data concerning the position of the critical point of oxygen concentration, that can be obtained from motionless fish using the flowing water method, are of limited value for an understanding of the metabolic rate of fish under natural conditions. The metabolic rate when a fish is active is more closely dependent upon the oxygen content of the environment than is its basal metabolism. In this sense Privolnev's data, in which are summarized, as it were, the results of a varying mobility and excitability, and show a varying degree of dependence of metabolism on the partial oxygen pressure in the environment, may reflect fairly accurately <u>relative</u> differences in the ecological and physiological characteristics of different freshwater fishes.

Short experiments cannot show how long fish can endure such oxygen concentrations in the environment as inhibit respiration. T. I. Privolnev supposes that "fish can endure inhibition of respiration or oxygen starvation for a long time, even months". This conclusion is very important for such problems of pisciculture as the conditions for survival of fish in a wintering pond, the shipping of fish, etc. However, in interpreting his results Privolnev failed to differentiate between the reduction in rate of oxygen consumption at the beginning of the experiment and the reduction that occurs when [<u>page 64</u>] the oxygen concentration in the environment drops below the critical point; hence this conclusion can scarcely be regarded as well founded. We consider it more accurate to imagine that fish can exist for a prolonged period at a reduced rate of oxygen consumption only if their metabolic level is lowered as the result of acclimation to a low environmental oxygen level.

Until recently nothing was known about how and to what extent acclimation to a reduced, or increased, oxygen content in water affects the metabolic level in fishes. For this reason the results obtained by A. G. Mints (1952) in a special study of this problem are of particular interest. In these experiments she kept fingerlings of several freshwater species (dace, perch, carp, tench, crucian carp) for a prolonged period at a constantly high (120-130% O_2) or a constantly low (8-10% O_2) environmental oxygen content. Measurements of the rate of oxygen consumption, made under normal conditions, showed that a few days after the beginning of the experiment the metabolic rate of fish that had lived under a reduced oxygen content began to decrease, and in the fish that lived at a high oxygen content the metabolic rate had begun to rise.

After 12-18 days a new steady metabolic level had been established. In the case of acclimation to a high environmental oxygen content, the metabolic level of tench was 55% higher than their original [page 65] metabolic level, perch were up by 39%, carp by 36%, crucian carp by 23.5%, and dace by 11%. Acclimation to a low environmental oxygen content was accompanied by lowering of the metabolic level of dace by 33%, of perch by 17%, tench by 15%, crucian carp by 12% and carp by 8%. The author associates the smallness of the depression of the metabolic level of crucian carp, tench and carp with the ecological peculiarities of these fish; since so low an environmental oxygen content is "almost usual" for them. A similar experiment was performed in which tench 2 years old were used (weight 102-138 g), in which the shifts in metabolism on acclimation to different oxygen conditions were less strongly developed (+30% and -10%). The change in the threshold concentration of oxygen on acclimation to different oxygen conditions was also determined. The threshold concentration at which asphyxiation occurs, in all the fish studied, changed in strict proportion to the change in metabolic level.

Similar results were obtained by N. D. Nikiforov (1953) when raising young salmon in two ponds. In one of the ponds the "constant O_2 content" was 5.5 mg/l, in the other it was 10.0-12.5 mg/l. The rate of oxygen consumption, measured at a high level of environmental oxygen content, was 206 mg/kg/hr for the fish reared in the first pond (average of 9 measurements), whereas for the second pond it was 361 mg O_2/kg/hour. It is too bad that the conditions and results of this interesting experiment were described with extreme carelessness. The experimental conditions are not stated, not even the temperature at which measurements were made(!), nor that at which the fish had been reared. It is not at all clear how a "constant O_2 content" could be achieved, or to what extent the other conditions in the experimental ponds were similar. Judging by the "weight of the young fish" quoted in [his] table 2, the rate of growth of the fish was practically the same in both ponds, which is hard to imagine in view of such different levels of metabolism. Furthermore, if it can be assumed that the laboratory measurements were carried out at a temperature not less than 14.5°, then in comparing them with the data from the same work shown in [our] Fig. 24, one is inclined to wonder at the extremely low metabolic rate of the fish in the first group, which is even lower than that of fish of greater weight raised in an aquarium.

Nevertheless, it cannot be denied that Nikiforov's data in general correspond very well with the results obtained by Mints, who showed that the acclimation of fish to different environmental oxygen contents is accompanied by corresponding changes in the level of metabolism, which in some cases can be rather large.

If the necessary expansion of the zone of oxygen adaptation cannot be achieved by lowering the metabolic level when there is a decrease in oxygen content under natural conditions, [page 66] fish have another means at their disposal for responding to the exigencies of the environment, namely, locomotory reactions. It is very important that under natural conditions fish often have a chance to avoid actively unfavourable oxygen levels by moving into parts of the environment which contain more dissolved oxygen. In studying the distribution and movement of fish in relation to oxygen distribution, Privolnev (1948) arrived at rather interesting and significant conclusions, after summarizing the observations by N. A. Mosevich on fish deaths from suffocation in the Ob River, the observations of G. D. Dalkeith on Lake Chana, and other data. He points out quite rightly that the time when the dead fish appear should not be regarded as the start of the oxygen famine; rather, it starts at the time when inhibition of respiration begins. Privolnev emphasizes that fish begin to leave a body of water in which serious oxygen deficiency is developing while there is still a fair amount of oxygen in the water. This makes it possible to predict the behaviour of different species of fish when a decrease of oxygen concentration sets in. For example, according to Privolnev very large concentrations of coregonid fishes should be expected when oxygen has decreased to 5 mg/l.

Of interest in this connection are some recently published experimental data which throw light on the reaction of fish to water with reduced oxygen content (Jones, 1952). For the experimental study of this problem an apparatus was used which makes it possible to create in a vessel two sharply separated zones of different dissolved oxygen contents. At a temperature of 13° the experimental fish--sticklebacks (Gasterosteus aculeatus)--readily swam into the water of low O_2 content, but owing to the difficulties of respiration that quickly set in, they became restless and returned again to the section of the vessel with high oxygen content, where they soon calmed down. At a low temperature (3°) dyspnoea set in more slowly, and the entire reaction required a longer time (5-6 min). The opposite was observed at 20°. Here dyspnoea set in so quickly that the fish usually failed to enter completely into the zone of low oxygen content. Experiments with minnows and young trout yielded the same results. These data indicate that, especially at a high temperature, reducing the dissolved oxygen content in water evokes locomotory reactions in fish, which under natural conditions act to concentrate them in places where the oxygen content is compatible with that to which they are acclimated.

In locomotory reactions of this type there is a regulatory role of the nervous system, which ensures an active selection of conditions that best meet the fish's oxygen requirements.

* * *

[page 67] It has been shown by experimental work that, when oxygen concentration in the water is reduced, the metabolic rate of a fish remains at a steady level until the oxygen content drops below a certain critical value below which metabolic rate is limited by the oxygen content of the environment and the mobility of the fish is suppressed. When, with continued lowering of the oxygen concentration, a "threshold value" insufficient to support metabolism has been reached, the fish begin to die.

The higher the metabolic level, the sooner the critical point is reached and the smaller the range of partial pressures of oxygen in the environment over which the metabolic rate remains constant. For this reason the size (age) of fish, their activity, and the temperature, all influence the nature of the relation between metabolism and environmental partial oxygen pressure.

Two factors are of great importance in understanding the influence of dissolved oxygen on the metabolic rate of fish under natural conditions: a change in their metabolic rate when they become acclimated to different oxygen conditions, and the locomotory responses by means of which fish can "select" conditions in keeping with their "zone of oxygen acclimation".

Chapter IV. [page 68]

The Influence of Certain Factors on the Metabolic Rate of Fish, and Diurnal Fluctuations in Metabolism

1. Significance of the ambient hydrogen ion concentration

Many other factors can influence the metabolic rate of fish besides temperature and partial pressure of oxygen, and concerning them comparatively little is known. The amount of carbon dioxide dissolved in water can scarcely be of any significance under ordinary conditions. It is known (Ivlev *et al.*, 1938) that only at quite a considerable carbon dioxide content does the latter begin to have a depressing effect on fish. Fry's (1947) straightforward data, obtained while studying threshold concentrations of oxygen for goldfish under different partial pressures of carbon dioxide, are of interest in this respect. It was shown that at average temperatures the threshold oxygen concentration rises rapidly only if the partial pressure of carbon dioxide reaches very high values (120-160 mm Hg). At low temperatures a rise in the threshold oxygen concentration occurs at a somewhat lower partial pressure of carbon dioxide. It is known that threshold concentrations are closely related to the metabolic level. Therefore there is no doubt that from these data one can also draw conclusions regarding the nature of the influence of carbon dioxide on metabolic rate.

The pH of the environment is of greater significance. Until recently reference has often been made to the work of Pereira (1924) in which an effect of pH upon fish respiration seemed to be indicated. However the primitive method used, and the careless presentation of the data, make it impossible to attach any importance to his data. The work of Powers (1923) also, who believed that oxygen consumption by herring (*Clupea pallasi*) attained its highest rate at an optimal pH of 7.66-7.78, is quite unconvincing.

More consistent data were obtained from *Sphaeroides* (*Tetraodon*) *maculatus*, which is a convenient subject for the study of respiration (Hall, 1931). The anatomical peculiarities of this species make it possible [page 69] to collect the water that passes through the gills by means of tubes inserted into the gill apertures. Under these somewhat artificial conditions it was found that when the pH was reduced from 8.5 to 6.5 the oxygen consumption rate was also greatly reduced.

Wiebe and his co-workers (1933) examined the rate of oxygen consumption of Huro floridiana over a range of pH values. A considerable number of measurements were carefully made by the flowing water method. Following the accelerated rate of oxygen consumption during the first few hours, the oxygen consumption rate of motionless fish became stabilized at exactly the same level at all the pH's studied (6.5, 7.5, 8.1, 9.4, 9.6, 9.7). In a subsequent work by the same author (1934) it was found for 14 species of fish that the threshold oxygen concentration is practically independent of pH until extreme values are reached, after which it rises rapidly. The pH range so defined is different for different fish. These data may be regarded as indirect but important evidence supporting the proposition that within the limits of pH that are normal for each species, the metabolic rate of fish is practically independent of pH.

What has been said refers to the effect, on metabolic rate, of the pH of the environment in which the fish were kept at the time the measurements were made. This kind of immediate effect of pH, such as can be detected in brief experiments, must be distinguished from the influence of a prolonged application of this factor. Unfortunately, this circumstance has not been taken into consideration by the authors who have studied this problem. However, Leiner (1937) observes that a reduction in metabolic rate at low pH values is most likely the outcome of some injury or damage. E. G. Svirenko (1937) discovered that if the pH is shifted towards the acid side beyond normal limits, the initial rise in the oxygen consumption rate, which apparently occurs as a result of exciting the fish, is followed by a marked reduction. Unfortunately the numerous measurements by this author, which were made under very many variations and combinations of ambient conditions, yielded such motley results as to defy any attempts at generalization. Lindroth's (1942) material also shows a reduced metabolic rate of pike at pH 5.6-5.9. Of special interest is the work of T. V. Novikova (1939), who made a special study, in Skadovsky's laboratory, of the metabolic rate of fish at various pH's during a prolonged experiment (7 days). Only average data, from 24 measurements each, are given for each pH value. From the average of the data obtained over the course of the experiment for 2 perch fingerlings, the oxygen consumption rate at pH 5.5 was 18% lower than at pH 7.4. [page 70] Carp fingerlings (2 specimens) under the same conditions showed a somewhat larger mean reduction in metabolic rate (by 33% and 22%). It is pointed out that "on the third day of holding the fish in acidified water (at pH 5.5) an increase in consumption of O_2 was observed". Though food was available, "during the experiment (7 days) the fish lost weight perceptibly". The frequency of respiratory movements was increased at reduced pH values. This presents a clear picture of the depressed physiological condition of the fish, which naturally was accompanied by a lowered metabolic rate. It is noteworthy that under such extreme conditions the reduction in the metabolic rate was relatively slight.

On the whole it must be concluded that the nature of the influence of pH on the metabolic rate of fish still needs clarification. The fragmentary data at hand do not contradict the opinion that within the limits of pH that are normal for the species, i.e. within the "zone of adaptation" to environmental pH, the metabolic rate of fish remains at practically a uniform level. This is in contrast to the frequency of respiratory movements and other indications that reflect the physiological mechanisms thanks to which it is possible to supply the organism with oxygen in an amount sufficient to satisfy the requirements of metabolism under environmental conditions that vary within the limits of what is "normal". We may conclude that the relatively small differences in pH which can arise when measuring the metabolic rate of fish do not, as a rule, affect the oxygen consumption rate.

2. The influence of the salinity of the environment

It is well known that among fishes there are wholly marine species and wholly freshwater species, and also species that during their life cycle move from the sea into a river or the reverse. Therefore, when considering the possible relationship between metabolic rate and salinity it is advisable to differentiate very clearly between different aspects of this problem. Firstly, we should find out whether the metabolic rate of fish which have salt water as their normal habitat differs from the metabolic rate of freshwater fish. If there is a difference, its direction and its extent must be established. A definite answer to this question will be given below, following the presentation of measurements of metabolism of marine and freshwater fishes (page 164).

Secondly, we should know whether the metabolic rate of each of these kinds of fish changes in relation to increase or decrease in salinity of the environment. If it changes, in which [page 71] direction does the change take place and to what degree? In this connection we must be ready for a different answer for different species of fish, or different stages of individual development, depending on the nature of their adaptation to the environment. Since in the last analysis we are trying to ascertain what the metabolic rate of the fish is under natural conditions, we must regard as of minor interest experiments in which a species is subjected to the action of solutions whose salinity exceeds the natural range of variation of this factor.

There is little factual material available to assist in finding an answer to the above question. Furthermore the authors who have been interested in clearing up the problem of the relation between fish metabolic rate and salinity of the environment have, as a rule, underestimated the complexity of the problem. Therefore it is often very difficult to make use of the results of their experiments, for conclusions of any kind. Only in recent works, for example that of E. A. Veselov (1949), is consideration given to the fact that one must distinguish between those changes in metabolism that occur immediately after a fish has been placed into an environment of different salinity (the primary acclimation [pervichnai͡a adaptatsii͡a] in Veselov's terminology) and the subsequent changes that accompany acclimation to the new conditions (Veselov's secondary [vtorichnai͡a] acclimation). I regard the terms suggested by Veselov as not entirely suitable; for it is not clear that we should talk about acclimation in the initial phase. There is no question of the value of his suggestion that it is necessary to distinguish primary changes in metabolism from those that arise over a much longer period of time in association with the acclimation to new conditions. It has been shown repeatedly that the initial changes in metabolic rate, which occur after placing fish in an environment of different salinity, will disappear and the metabolic rate will approach normal. Such data are found in the work of Keys (1931) on the marine fish *Fundulus parvipinnis*, whose metabolic rate decreased when it was placed in fresh water. However, in the specimens that survived in fresh water, the normal metabolic rate was soon restored. Another author, who used the related *Fundulus heteroclitus*, discovered that their rate of oxygen consumption in Ringer's solution and in fresh water were the same (Maloeuf, 1937). Leiner (1938), on the basis of experiments with sea-horses, maintains that the great rise in the metabolic rate which first follows a rise or fall in the osmotic pressure in the environment persists for only a short time, and afterward the normal metabolic rate is re-established. Veselov reports similar data for crucian carp. It is characteristic that at a salinity of 7.8‰, [*page 72*] which is harmless to crucian carp, their metabolic rate returns to normal after a brief rise; whereas if the salinity amounts to 15.6‰, at which point "30-40% of crucian carp die" in summer, the metabolic rate remains at a low level for a long time. The results obtained by A. L. Bri͡ukhatova (1939) in Skadovsky's laboratory are very interesting. It was in her investigations that the point was first raised of the necessity of studying the influence of salinity on metabolism of fish in prolonged experiments. According to Bri͡ukhatova's data (table 8 and others) it can be seen that the metabolic rate of carp which were kept for a long time in water with a high salinity (9-13%) showed no noticeable departure from "normal" after the initial reduction. As in the experiments of Keys, even at a limiting level of salinity (9-13%), at which most of the fish could not survive for any length of time, the metabolic rate of the surviving specimens did not differ from the normal rate.

In the light of these results, the short term experiments of various authors who have described examples of change in rate of oxygen consumption when fish were placed in an environment of different salinity (Raffy, 1930; Halsband, 1953; Markova, 1949) are of no particular interest, the more so as they involve comparatively small shifts in the metabolic level, whose reality was not always proven. Apparently Schlieper (1936) is the only one who has attempted to discuss theoretically the probable ways in which salinity can influence metabolism. According to Schlieper's "hydration theory", salinity affects the metabolic level of fish and other aquatic animals through changes in the degree of hydration of their tissues as affected by osmotic forces. Although there is some basis for the assertion that an increased water content in the tissues is associated with increased metabolism, nevertheless to apply the crudely mechanistic notions of Schlieper to the metabolism of an entire organism under conditions which are normal for it, is to disagree with all the known facts, as Veselov (1949) has pointed out. The attempts at experimental confirmation of this theory which have been made by Schlieper and his students (Halsband, 1953) are very weak methodically, and the precise meaning of the data obtained in their experiments is quite unclear. For example, in Halsband's experiments with trout an increase in the rate of oxygen consumption under the influence of saline solution was observed only at 15°, whereas at 5° and 10° a reduction in metabolic rate occurred.

In this case, as in all the other examples known to me where changes in metabolism under the influence of changes in environmental salinity were obtained experimentally, there is no analysis of the immediate causes of the effect observed. The effect might result from a rise in the level of tissue respiration [page 73] and of resting metabolism, or from an increase in excitement or movement of the fish.

The shortness of the majority of the experiments conducted, and the paucity and arbitrary selection of material for study, make it impossible to ascertain whether the metabolic level of fish of a given species differs when it is fully acclimated to different salinities; nor can we know what is the reaction, in this respect, of different species of fish, or of different stages of the development of the same fish.

The only conclusion that one can arrive at on the basis of the material on hand is that considerable changes can take place in the metabolic rate of fish as a result of sudden transfer to an environment with a different salinity. However the metabolic rate returns to normal, in many cases at least, as a result of subsequent acclimation to the new conditions.

3. Diurnal fluctuations in the metabolism of fishes

A number of authors have shown that the metabolic rate of fish varies regularly with time throughout the 24-hour day, and that these differences can be quite considerable. Thus the results of measurements of respiration can also depend on what time of day they are made. However some authors, on the basis of their own experiments, deny the existence of diurnal differences in the metabolic rate in fish. It is interesting that Wells in his 1935 paper concurs with this opinion, whereas from the results of his own measurements published in the same article it is possible to prove conclusively the importance of diurnal fluctuations in metabolic rate (Fig. 14).

In reviews and text books it is usually stated that Clausen (1933, 1936) established the existence of diurnal fluctuations in the metabolic rate of fish. This statement needs qualification. It is true that in a paper dealing specially with this problem Clausen gives the results of successive hourly measurements of the oxygen consumption rate of fish made throughout the 24-hour day. He used the flowing water method, with the respiration chamber darkened by a dark cloth. The fish were placed in the respiration chamber 12 hours prior to the measurements. Three of the 8 species of river fish that were tested showed no consistent differences in metabolic rate over a 24-hour period. For the others there were, in the author's opinion, regular diurnal fluctuations the nature of which differed from species to species. Experimental data are furnished for only two species, and these only in graphical form. The graphs show very great divergences between the results of adjacent measurements, which makes it difficult to demonstrate the reality of diurnal trends. It must be said [page 74] that, of the two examples given, only the first, referring to largemouth bass (Huro salmoides, weighing 40-50 g), indicates the existence of regular diurnal differences in metabolic rate sufficiently convincingly. The largemouth bass used in Clausen's experiments showed two maxima in the rate of oxygen consumption, namely, in the morning (approximately at 6 o'clock) and in the evening (at 21 o'clock). The maximum oxygen consumption rate was about twice as high as the minimum. Among the irregular fluctuations of the metabolic rate on the second graph it is very difficult to distinguish diurnal differences with any confidence. It seems that in this species (Ameiurus melas, weighing 35-60 g) a diurnal trend was suggested only by a slightly lower metabolic rate during the day. It is improbable that diurnal fluctuations were manifested any more clearly in the metabolism of the fish for which experimental data are not furnished by the author.

Therefore in citing Clausen's data for largemouth bass it is incorrect to ascribe general significance to them, as is usually done in reviews, or to regard them as a representative example of the diurnal fluctuation in metabolism of fish in general. We saw that in Clausen's material they are rather the exception than the rule. In summarizing his observations, Clausen writes that diurnal fluctuations in rate of oxygen consumption are apparent only in fish which inhabit sections of the river where the current is slow and which have a relatively low metabolic rate. Fish in the upper reaches of rivers, where the current is swifter, have a higher metabolic rate but they exhibit no diurnal differences.

Oya and Kimata (1938) demonstrated the existence of well developed diurnal fluctuations in the metabolic rate of carp of 10-20 g. According to these Japanese authors' data the minimum rate of oxygen consumption in carp occurs at night. In the morning the metabolic rate rises rapidly and reaches a narrow peak at 14 o'clock, at which time the metabolic rate exceeds the minimum by 1.5-2 times. The flowing water method was used and a dark cloth was wrapped around the respirometer. Apparently the fish were kept in darkness during the whole experiment. It is not clear whether other disturbances (vibrations, etc.) were eliminated, which under ordinary laboratory conditions also have a diurnal rhythm.

Another author has published the results of hourly measurements of the rate of oxygen consumption of two different species of fish (Ictalurus lacustris punctatus and Schilbeodes nocturnus), which however were restricted to the hours of daylight (Higginbotham, 1947; Ecol. 28, 462). The metabolic rate increased rapidly in the evening, especially with the second species. The author relates this to an increase in activity. Some very large [page 75] differences between the metabolic rates, and other peculiarities of these data, make it possible to agree with the author that his data are not sufficient to warrant definite conclusions regarding the nature of the diurnal fluctuations in fish metabolic rate. Diurnal differences in the oxygen consumption rate of fingerling Salvelinus fontinalis, measured at 5°, are shown by Graham (1949). According to her data the lowest metabolic rate in this species occurs during the night.

Soviet authors have given a great deal of attention to diurnal fluctuations in the metabolic rate of fish. They fully appreciate the need to reckon with this phenomenon when studying the many ecological and physiological characteristics of fish, which are of importance both practically and theoretically (Olifan, 1940, 1940a; Poliakov, 1940).

In a work devoted to a study of the "diurnal rhythm of respiration in fish larvae", V. I. Olifan quotes several of her numerous series of diurnal observations of the rate of oxygen consumption of larvae of sevriuga, whitefish, pike and wild carp of different ages. Olifan's conclusions are very unusual; they differ radically from what is known about this phenomenon from the data of other authors, and also from what would be expected from existing knowledge of fish metabolism. Olifan believes that she has shown that the metabolic rate of fish larvae, over the 24-hour day, exhibit sharp rhythmic fluctuations, so that "during the morning and evening hours respiration rises sharply, whereas during the night and during the day it as sharply declines". However, in describing the data for the individual species she indicates that sevriuga larvae more than 20 days old "also show a third maximum of respiration at the beginning of the day"; in osëtr larvae a maximum occurs "at 12-14 o'clock also"; in pike 25 days old "a third peak in respiration occurs at the beginning of the day"; and in whitefish larvae it occurs "also at the beginning of the day (13-14 o'clock)". It is indicated that "very young carp larvae, in contrast to those of sturgeons and pike, also have a third peak in respiration". In keeping with these beliefs, in presenting her data graphically Olifan joins the empirically obtained points with curves of various forms, having many peaks, so that often the total number of maxima and minima on the curves is equal to or very close to the number of empirically obtained points. Neither is Olifan embarrassed by certain peculiar features of her data, for example the fact that the curves showing the diurnal "rhythm" for carp larvae indicate that the larvae do not respire at all during some hours of the day! Olifan's data have not been confirmed by anyone, but her conclusions have been repeatedly quoted by other authors. This has compelled me to give some attention to them, although it is quite clear that to a large extent they are the result of the author's uncritical attitude [page 76] in using quantitative methods, insufficient standardization of conditions, and other similar causes. Hence there is no reason to agree with Olifan when she says that her data should be taken into consideration when calculating the water supply for ponds used in fish culture. Olifan is of the opinion that the diurnal "rhythm of respiration" of fish larvae is not related to variation in degree of the activity of the young fish. Furthermore, in her opinion, light is "the factor of the external environment which controls the phenomenon of the diurnal cycle of metabolism". It is not clear how, under the influence of light, the maxima of the metabolic rate arise at different hours of the 24-hour day if, as Olifan believes, the diurnal "rhythmicity" of metabolism has nothing to do with behaviour. E. G. Svirenko (1948), who studied respiration in young sturgeons, could not discover the sharp diurnal differences in the metabolic rate which were described by Olifan for the same species.

Yu. D. Poli͡akov (1940), who made a thorough study of the diurnal course of respiration of fish, used young tench weighing 0.2-0.9 g in his experiments. A manometric differential respirometer equipped with an automatic recording device, constructed by the author, was used for measuring the rate of oxygen consumption. One valuable aspect of Poliākov's work is the fact that the experiments were conducted under three types of light condition: natural illumination, continuous illumination and continuous darkness.

Using only part of the data he obtained, Poliākov trys to show that under natural illumination 4 maxima and 4 minima in the metabolic rate can be observed during the 24-hour day. However he writes: "The nocturnal maximum is not uniform among the different experiments. It sometimes occurs before midnight, sometimes later. At times the nocturnal maximum is steep and prolonged and at other times it is barely noticeable. In two experiments it was double." Likewise in the daytime, "absorption [pogloshchenie] proceeds irregularly". The morning and evening maxima, in this author's opinion, are those most plainly indicated. However even here "in some individual experiments the differences show up much more sharply, and it appears that some maxima exceed the minima by 10 or even 20 times". This last circumstance makes one pause. The fact is, as is shown below (page 168), that even for the greatest possible speed of movement the active metabolism of fish does not exceed the resting metabolism to any such degree.

We consider it very likely that the radical fluctuations in the oxygen consumption rate observed by Poliākov are due, to a considerable extent, to his particular method of making the measurements. In using manometric methods, the pressure or the volume of air [oxygen?] in the respirometer above the water containing the fish is the property that is directly measured. The pressure in the gaseous phase at each moment depends not only [page 77] upon the oxygen content of the water containing the fish, but also upon the rate of equilibration of partial pressures of gases between the water and the air in the respirometer. Under these conditions, if the fish begin to move after a period of rest, the manometer records not only the increased metabolic rate during motion, but also the sharply increased rate of equilibration of the partial pressures as a result of the stirring of the water when the fish are in motion. Because of this, when manometric measurements are made, as in the experiments of Poliākov and Olifan, sharp fluctuations in the readings do not at all indicate similar sharp fluctuations in the rate of oxygen consumption, because the water is not stirred during periods when the fish are relatively quiet; they merely indicate that periods of relative quiet follow periods of activity. Poliākov points out that the evening and morning maxima "correspond well with information on the behaviour and feeding of these animals".

The series conducted in darkness, in his opinion, led to lower mean values "as a result of smoothing out the maxima". However, this cannot be identified in the numerical data. For example, according to the data from 7 experiments (17 readings) presented in his table 3, the mean metabolic rate in the dark is 64.2 mm^3 O_2 per gram per hour at 17°; but under natural light it is 65.9, according to the mean value from 42 readings (table 1). With continuous illumination the mean consumption rate, from 24 values (table 2), was 88.6 mm^3 O_2, i.e. it was considerably higher than under natural illumination.

All the abovementioned data indicate that in some cases it is possible to discover noticeable diurnal differences in metabolic rate by means of a sufficiently long series of laboratory observations. For our purposes it would be interesting to know to what extent these data could also be applied to natural conditions. Some interest attaches to the observations of Yablonskaîa (1951) on the oxygen consumption rate of verkhovka (Leucaspius delineatus) kept in an enclosed part of a lake under conditions very similar to natural conditions. Measurements by the sealed vessel method were made in the morning (4-7 o'clock), during the day (11-13 o'clock), in the evening (17-19 o'clock) and at night (21-24 o'clock). In 6 experiments no diurnal differences in metabolic rate could be discovered. The somewhat greater metabolic rate during the day was evidently caused by the higher temperature of the water at that time.

M. N. Krivobok (1953) measured the respiration rate of young carp 4 times during the 24-hour day (morning, daytime, evening and night). From the average of 9 series of measurements the mean temperature of the water during these periods was equal to 22.1°, [page 78] 28.1°, 27.8° and 23.1°. The oxygen consumption rates were 0.747, 1.020, 1.023 and 0.607 mg per gram per hour. On conversion to 20° this comes to 0.626, 0.530, 0.543 and 0.467 mg per gram per hour. The greatest deviations from the mean do not exceed 15%. It is evident that in this case also there is no reason to speak of diurnal deviations in metabolic rate that are of any significance.

Similar results were obtained by G. G. Winberg and L. E. Khartova (1953), who measured the oxygen consumption rate of young carp by the same method (Fig. 26). This was done under conditions that were perhaps close to natural conditions. During the test the experimental jars were submerged in the water of the pond from which the young fish and the water for the experiment had been taken. All the measurements were carried out in parallel, under natural light and in darkness. The results from 81 pairs of parallel measurements did not show any differences in the oxygen consumption rate either in daylight or in darkness. Under illumination the metabolic rate was 0.636±0.027 mm^3 O_2/mg/hour at 20°, in the dark it was 0.618±0.024; i.e. the difference between the means was even smaller than its standard error (±0.036). Such a result can serve as convincing evidence of the fact that light has no direct effect upon the metabolic rate of carp, within the range of natural illumination. The work of E. A. Yablonskaîa on the influence of light upon the growth and feeding of fingerling mirror carp agrees well with the above. G. S. Karzinkin (1952, page 209) states that "we could not confirm any change in the volume of [oxygen] consumption by carp under the influence of light". It seems that this applies to many other fish. In passing, we will point out that the literature contains only scattered references to metabolic rate of fish under different lighting conditions. For example Pütter (1910), and also Wells (1935), deny that light, of itself, has any effect upon metabolic rate. Obviously this does not apply to cases where the light, by stimulating [page 79] the activity of the fish, can increase its metabolic rate indirectly.

The data of Yablonskaīā, Krivobok, and Winberg and Khartova are as yet insufficient to settle the importance of diurnal fluctuations of metabolism under natural conditions. However, they have shown that when metabolism is followed over a 24-hour day it is not certain that appreciable differences in metabolic rate will be encountered. Attention should be given to the fact that the sealed vessel method has been used in recent works. Thus the fish were not kept uninterruptedly in the respirometers, as is true when the flowing water method is used, but were taken from natural conditions just prior to each measurement. The unavoidable excitement associated with this may have concealed any diurnal differences in metabolism to some extent.

No matter what the proximate cause of diurnal fluctuations in metabolic rate, in their origin and biological significance they are associated with the diurnal rhythm of the complex of various factors in the environment which determine the rhythm of activity and feeding.

The nature of the diurnal activity of fish was studied by Spencer (1939) by means of an "ichthyometer", a device using a mechanical recorder. He recorded movements of carp, goldfish and several other species, when tethered by a thread. The author maintains, without showing the results of the recordings, that each species of fish has its own definite type of activity, that some species are active during the day, others are active at night, that seasonal and age differences exist in the types of activity and that large individual differences occur. Data have also been published by Hard (1942) which indicate that the variation in diurnal activity associated with the feeding periods is retained also in the dark, in the case of salmon and trout. Especially interesting are the results obtained in studying the diurnal activity of goldfish by means of an electrical recording of the disturbances in the water caused by their movements (Spoor, 1946). The aquarium containing the fish was kept in a separate room, which made it possible to isolate the fish effectively from secondary disturbances and to control lighting and other conditions. Continuous recording by machines located in the

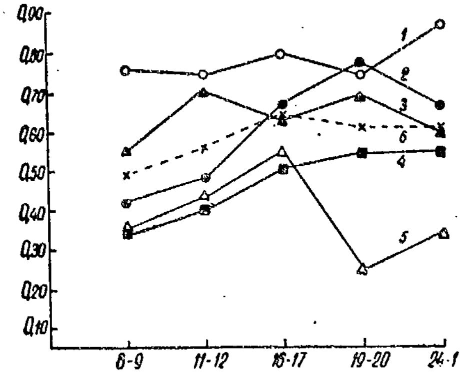

Fig. 26 [page 78]

Metabolic rate of young carp during various hours of the day.

1- measurements of June 14, 1951, average weight of fish 3.6 mg; 2- June 16, weight 7.0 mg; 3- June 28, weight 24.7 mg; 4- June 21, weight 51.6 mg; 5- July 20, weight 2620 mg; 6- average data for all measurements. Abscissa--time of the measurements. Ordinate--oxygen consumption in cubic mm/mg/hour, adjusted to 20° (Winberg and Khartova, 1953).

adjoining room was maintained for a considerable length of time (up to many months). It was found that different individuals display different types of diurnal activity. One can differentiate between three main types of fish behaviour: 1) arhythmic, 2) active during the day, 3) active at night. It was shown that light affects the type of activity and that in constant light (also in constant darkness, or with interrupted illumination) the sequence of periods of activity and of rest is retained for a long time. [page 80] Most important is the fact that the type of activity can change in an individual in what seems to be a strictly constant environment. It was also established that fish are very sensitive to various disturbances and react strongly to sounds and even to the presence of an observer in the room.

Each degree of activity has its own level of metabolic rate (see Chapter IX), hence, all that has been said about the diurnal rhythm of activity can certainly also be applied to changes in metabolic rate over the 24 hours. Consequently, there is not and cannot be one single type of diurnal pattern of metabolism, common to all fishes. Different species and even different individuals of a species can present an altogether different picture of diurnal fluctuation in metabolic rate. It seems that the diurnal differences in metabolism which have developed as a response to the rhythm of environmental conditions are to a certain extent fixed, but only in the sense that the alternation of periods of higher and lower metabolism can be retained under constant conditions for some limited period of time. With change in the rhythm of diurnal change of light and other stimuli, the type of diurnal fluctuation in metabolism changes accordingly. There is no basis whatever for postulating the existence of "rhythmic" fluctuations in metabolic rate that arise independently of [environmental] conditions. The diurnal changes in rate of oxygen consumption that are actually observed have their origin in the daily rhythm of light and dark and a complex of other natural factors that act not directly, but through changes in the pattern of the diurnal change in periods of rest and activity. The diurnal fluctuations in metabolic rate that are brought to light in a laboratory using the flowing water method, when the fish remains for a long time in a "motionless" position and is artificially isolated from many stimuli, are to some extent artificial. Under natural conditions, when there are large changes between periods of activity and rest, diurnal differences in metabolism may be much better developed. On the other hand, under natural conditions the fish are subject to the influence of many different factors, which can greatly modify the diurnal fluctuations in metabolism even in organisms in which an alternation of periods of greater and lesser activity is inherent. There is no doubt that there are fish without any definite pattern of diurnal activity, and for them there is no reason at all to expect regular diurnal differences in the metabolic rate.

Thus the entire problem of diurnal fluctuations in the metabolic rate of fish, from our point of view, is not an independent problem. It will be clarified in the course of a study of the laws governing the behaviour of fish during the daily cycle, and the relation of metabolic rate to the degree of activity and speed of motion.

4. The influence of periods of fasting and various other prior conditions upon the metabolic rate of fish [page 81]

The results of measurements of the rate of respiration of fish depend, firstly, on the conditions of the medium in which the fish are held during the experiment, that is, upon factors that affect the fish directly during the time spent in the respiration chamber (temperature, oxygen content, etc.); secondly, they depend upon conditions that precede the experiment, which determine to a considerable extent the physiological condition of the fish during the time of the measurements; and thirdly, they depend upon the specific characteristics of the material: its species, sex, stage of development, size, and so on.

It is the role of factors of the first group, mainly, that has been considered above. Now we must see to what extent a fish's metabolic rate can depend, also, upon its physiological state during the time of the measurements, as this is determined by conditions previous to the experiment. First among these conditions is nutrition. In comparing the results of measurements of respiration, one must know to what extent feeding and periods of hunger prior to the experiment can affect the fish's metabolic rate.

It is not hard to find in the literature many individual comments concerning the effect of food or starvation upon the respiration rate of fish, but there are no specific systematic investigations of this problem, except the thorough work of Smith (1935) on a rather special species--the lungfish <u>Protopterus aethiopicus</u>.

Very interesting data were obtained from this extremely unusual subject, which was studied after it had been kept in an aquarium for a considerable time. It was found that the metabolic rate of <u>Protopterus</u>, which was measured by its rate of oxygen consumption and production of carbon dioxide, ammonia gas and urea, is reduced rapidly during the very first days of starvation. As early as the seventh day of starvation the metabolism has been reduced by 50%. After 300 days of starvation the metabolic rate was only 10-20% of the original. According to the calculations of the author, the survival time under starvation is increased 4-6 times by reducing the metabolic rate. Smith points out that this fish exhibits a steady metabolic level only when fed regularly. It is clear that all these peculiarities, which are not found at all in other fish that have been studied in this respect, are a specific adaptation that facilitates survival during the long periods of unfavourable conditions that are characteristic of the natural habitat of [page 82] lungfishes. Although the metabolism of the overwhelming majority of fishes reacts to starvation altogether differently, the observations of Smith are interesting in that they demonstrate an extreme case of adaptation to special conditions.

It has been pointed out repeatedly that starvation is accompanied by a reduction of the metabolic level of fish. Pütter (1909) published several series of observations on the oxygen consumption rate of various marine fishes during prolonged periods of starvation. In one fish the oxygen consumption rate during 40-50 days of starvation was reduced by 2-3 times, whereas in other species, for example Scorpaena porcus, during the same period of starvation the rate of oxygen consumption remained constant. In view of the considerable loss in weight (from 16.3 to 12.1 g) this even implies a rise in the metabolic rate.

In the well known work of Lindstedt (1914) the influence of starvation upon the metabolism of tench is specially discussed. One can see from the data of the tables on page 234 of this work that during the first period of measurement (16.IV-8.V) the mean metabolic rate of tench, when adjusted to 20°, was 84.8 ml O_2/kg/hour, whereas during the second period, after 1½-2 months of starvation (5-17.VI), it fell to 66.0, i.e. it was lower by 29%. The same author points out that feeding trout increases their metabolic rate by 22-26%. Similar indications of a reduction in metabolic rate during starvation are encountered in the works of Raffy (1933), A. G. Mints (1953), E. G. Svirenko (1948) and others. According to Mints' data, prolonged starvation of young tench (0.6-1.5 g) and crucian carp (4.2-5.7 g) reduces metabolism by 27%, on an average. According to A. T. Pozhitkov (1939), after a 24-hour period of starvation (the weight is not mentioned!) a crucian carp's metabolic rate is only 76% of the initial rate. After 20 days of starvation it is 67% of the initial rate and the loss in weight has been 4%. These data and similar material by other authors give an idea of the extent to which metabolic rate of fish can be reduced by starvation. These examples show that even in cases where a reduction of metabolic rate by starvation is noticeable, this reduction is comparatively slight during the first days of starvation. Many authors have described cases in which throughout many days of starvation it was not possible to detect any reduction of the metabolic rate. In the classic work of Ege and Krogh (1914) it was observed that the respiration of a starving goldfish remained at one and the same level during the whole period of the observations, which lasted about a month. T. V. Novikova observes (1939) that in her data, as in those of Pozhitkov, the respiration rate of the fish remained constant during the period from the 2nd to the 7th day of starvation.

[page 83] It was mentioned above that the authors who have used the flowing water method have attempted to measure the so-called basal metabolic rate, which they regarded as the metabolic level that is established after a prolonged stay, often lasting many days, of the motionless fish in the respirometer. In these cases it is stated repeatedly that the metabolic rate of the fish used remained at the same level throughout the experiment, regardless of starvation. Wells (1935) in particular, who used the rather active fish Girella nigricans, points out that for 7 days after the last feeding the metabolism remained at the same level. Smith and Matthews (1948), experimenting with Bathystoma sp., kept their fish in a respirometer for up to 19 days and discovered that in this species the metabolic rate remained constant even when a loss in weight occurred from starvation. However, these same authors point out that when Fundulus heteroclitus is kept in a respirometer for many days the metabolism does not level off, but falls gradually (Matthews and Smith, 1947).

The fact that it is with the flowing water method, which safeguards the immobility of the experimental fish, that examples of a stable metabolic level during starvation have been encountered, makes one think that the reduction in metabolic rate during starvation which is observed using other methods in which the fish can move freely (Lindstedt and others), is at least partially associated with more languid movement on the part of fish that have been starved for a long time.

Inasmuch as most of the data used later on were obtained with fish kept for relatively short periods in respirometers--periods measured in hours rather than days--it is evident from the material cited that the starvation of fish used in experiments of such relatively short duration could not noticeably affect their metabolic rate. For most fish the possible reduction during the experiment is entirely secondary in comparison with the reduction in the metabolic rate during the first few hours after they are placed in the respirometer. This latter is to be regarded as a result of the "quieting down" of the fish.

For all the scarcity of material concerning the effect of starvation on metabolic rate, it is possible to get some idea of the influence of this factor. Concerning many other factors which can influence the physiological condition of fish, and thereby also the metabolic rate, extremely little is known. In fact, there are only isolated indications, that do not suffice for any kind of generalization. For example there are no recent data which would indicate to what extent respiration of fish increases after feeding. The older data on this question, for example those of Lindstedt, [page 84] were obtained under conditions which do not exclude the possibility of an indirect influence of the feeding on the measurements due to an increase in the activity of the fish, or by other means. It is also quite uncertain how rate of respiration changes in relation to the various stages of sexual maturity and reproduction. Lindstedt (1914) has data indicating that the metabolic rate of motionless pike with mature [running] eggs was certainly no higher, possibly a little lower, than normal. However, it is quite possible that weakened specimens were used in the experiment. On the other hand, T. I. Privolnev (1948) remarks: "Research in our laboratory has shown that the respiration rate rose when the gonads matured, in bream (Veselov), muksun (Kharchenko and Markova), and peliad (Kharchenko and Shirkova)." A. P. Shcherbakov found no difference in the level of respiration among lampreys in stage IV of maturity, having a distended abdomen. Maksudov maintains that in Gambusia the respiration rate declines after the birth of the young, but this is not sufficiently supported by his material. Raffy (1930) describes the opposite situation for another viviparous fish, Girardinus. In this case after the birth of the progeny the rate of oxygen consumption per fish remained the same as that of pregnant females, in spite of a loss in weight of 14%. It may be mentioned in passing that according to available data the castration of fish is not reflected in their oxygen consumption rate (Ermakov and Medvedeva, 1934; Hasler, 1942). It was also noticed that the small changes in rate of respiration which can be observed in the later stages of the metamorphosis of lampreys are not on the same scale at all as the tremendous internal morphological changes that occur at that time (Leach, 1946).

In studying the metabolic rate at different stages of the sexual and reproductive cycle, it is necessary to distinguish possible changes in the basal metabolic level from those differences in the oxygen consumption rate that may depend, for example, upon the greater excitability or activity of the fish during the pre-spawning or spawning periods. There are no data available yet that would make it possible to study this question from this point of view. Quite probably the greater excitability and liveliness of a male Lebistes is the reason for the great difference between the metabolic rates of males and females of this species, noticed by Raffy, who points out that this difference is large enough that it cannot be ascribed entirely to the smaller size of the males. Wells (1935a) discovered no difference in the respiration rate of male and female Fundulus parvipinnis.

Many of the published materials and statements can be used only with difficulty to determine the nature of the relationship between respiration and whatever other factor is being examined. Often not enough attention [page 85] is given to the possible role of concomitant or subsidiary factors. Furthermore, it is often forgotten that differences in metabolic rate can arise simply because of differences in size of the subjects used in the experiments. This latter factor, the dependence of metabolic rate upon size (weight) of the fish, is of especially great importance. If this factor is disregarded, then it is impossible to obtain any reliable information regarding the influence on metabolism of age, stage of development, systematic position, or ecological adaptation to conditions of the natural habitat characteristic of each species. Therefore, before examining these important questions it is necessary to determine what the quantitative relationship is between the metabolic rate of fish and their size.

Chapter V. [page 86]

Metabolic Rate and Total Body Size in Fish

1. The "surface law" in fish

As early as 1877, in the first thorough study of fish metabolic rates, Jolyet and Regnard called attention to the fact that the rate of oxygen consumption of fish increases as their size decreases. They included the overall size of the fish among the most important factors determining metabolic rate--in which category they placed temperature, state of nutrition, size and activity, besides species differences. Even earlier Quinquaud (1873) had written no less definitely concerning the importance of size, as follows: "The relative intensity of respiration in fish decreases as weight increases." Quinquaud also believed that it was this factor, and not species individuality, which accounted for the differences he observed in the rate of oxygen consumption of various fishes. In subsequent years many people have given attention to the inverse relationship between fish metabolic rates and size, often discovering anew this long-familiar principle, which in one way or another is exhibited by the most diverse groups in the animal kingdom.

We must now investigate the quantitative nature of the relation of metabolic rate to size in fish. At first this question was dealt with in terms of a discussion of the applicability of the so-called "surface law" to fish. According to this law, the metabolic rate of animals of different sizes is proportional to a conventional index of their surface area, taken as the square of the cube root of the weight, i.e. the weight raised to the power $2/3 = 0.67$. The approximate absolute magnitude of the surface of the body of the fish (P) is obtained by multiplying the weight, raised to the power $2/3$, by some proportionality coefficient (A). The numerical value of A is equal to the surface of the body of the fish (of a given shape) having unit weight:

$$P = A\,w^{2/3}$$

When this method of calculation is used, the surface will be in square decimeters if the weight is in kg; if the weight is in grams, the surface will be in square centimeters.

[page 87] The magnitude of the proportionality coefficient has been determined by a number of authors. According to Lindstedt (1914) it lies between the limits 10 to 13 for various freshwater fishes. Rubner (1924) uses the figure 9 in

his computations. For various sizes of Scyllium cassicula, one of the sharks, the values 7-8 were found empirically (Buytendijk, 1910). In a special work Gray (1953) quotes determinations of the value A for 39 species of fish of very varied systematic position. According to his data, A varies within the limits 6.7 to 15.3 for different species, i.e. more than twice. This means that even in a case where metabolism was strictly proportional to the actual area of the surface of the body, it is possible to obtain values that differ by more than two times when comparing the metabolism of different species, if the conventional expression for the surface ($w^{2/3}$) is used without taking into account differences in the proportionality coefficient. Conversely, if the metabolism of two fish of different shapes has the same numerical value when expressed in terms of the conventional surface, or, more generally, to the weight raised to a certain power, their metabolic rates can differ importantly when computed per unit of actual surface.

This makes it plain that if metabolic rate is calculated on the basis of the conventional surface, we will obtain comparable values only in situations where it is possible to neglect differences in shape, for example when comparing differences in size[1] within a single species.

Zuntz (1901) believed that fish metabolism follows the surface law, on the basis of Knauthe's data on the metabolic rate of carp. Lindstedt (1914) interprets the results of a study of the respiration of various freshwater fishes from the same point of view. Rubner tried to prove that the surface law is applicable also to fish, by using the results of calorimetric measurements of metabolism of goldfish and sticklebacks and by using calculations of the metabolism of tench after the fish had lost weight from starvation. However, Rubner points out specially that he does not believe it possible to ascribe any causal character to this relationship. Bourdien (1932), who quotes only a few summary values, writes that in the three species of freshwater fish studied by him the metabolism is proportional to the surface. Most recently, Bertalanffy has maintained (1951) that the respiration of fish is proportional to surface. Bertalanffy quotes his own measurements of the oxygen consumption rate of Lebistes reticulatus of various sizes (weighing about 30 to 650 mg), which in his opinion support this view.

It is also not difficult to find in the literature statements by authors who believe that the relationship between

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[1] [literally "age differences of the sizes"--vozrastnye razlichiia razmerov. The possibility of effects of age, independently of size, is discussed and rejected later (page 144 of the Russian text)--hence it cannot be intended here.]

metabolism and size in fish cannot be expressed well by the surface law. In order to test the applicability of this law to [page 88] the metabolism of poikilothermic marine animals, Montuori (1907, 1913) conducted a large number of measurements on the rate of oxygen consumption of fish and various marine invertebrates. His much-quoted data are actually not at all suitable for any conclusions of a quantitative nature, as will be shown below. Very variable results were obtained because of his primitive technique and disregard of the physiological conditions of the experiment. Furthermore, Montuori failed to avoid numerous errors in his calculations, with the result that in many cases the oxygen absorption rates calculated on the basis of a unit of weight, those calculated for the whole fish, and the actual fish weights, are not consistent among themselves--as Zeuthen (1947) has pointed out. All Montuori's data are shown in Fig. 27. As compared with comparable data of other authors, an unusually great scatter of the points is evident. There is a particularly large discrepancy in the results of the measurements of the oxygen consumption made with fish of certain species, for example the eel. The data of other authors will be presented in subsequent chapters (Fig. 28-43).

[page 89] Special observations to test the applicability of the surface law to fish were made on Scyllium cassicula, a small shark (Buytendijk, 1910). Five measurements of oxygen consumption of sharks weighing from 14 to 260 g showed that in this case the larger fish consumed relatively more oxygen per unit of surface than the smaller fish, i.e. the metabolic rate decreased more slowly than the relative surface increased, with growth in size. It is easily seen from the data of this work that respiration was proportional to weight raised to the power 0.8 (Fig. 43). Leiner (1937), from measurements made by the manometric method, comes to the conclusion that the rate of respiration of the sea-horse decreases as the size increases. However, this decrease is not proportional to the relative surface.

Terroine and Delpech (1931), regarding the evidence for the applicability of the surface law to fish as unconvincing, undertook investigations to clear up this question. However, they used a very unusual method for "immobilizing" their fish, namely, tying them to a board(!); apparently for this reason, and perhaps others, they obtained completely unrepresentative data for the rate of respiration of tench and eels of various sizes. It is enough to say that tench weighing 218 and 225 g consumed respectively 22.2 and 29.0 mg O_2 per hour, whereas tench that weighed considerably more (378 and 381 g) consumed less oxygen during the same time (19.9 and 18.8 mg). Even more discordant are the values quoted by these authors for the respiration of the eel. For example, eels weighing 162 to 1800 g consumed 7.7 to 11.3 mg O_2 per kg at 20° according to their table 6. From the numerous and convincing data of the many authors quoted below (Fig. 36) there is no doubt that the actual rate of metabolism for eels, as for other fish of the same size, is at least 10 times higher. The scattered state of published data on the respiration rate of fish, and absence of any critical summary, have made it possible for the measurements of Terroine and Delpech to still be quoted up to quite recent times; they have even been used to cast doubt on Raffy's data, as was done by Zeuthen (1947). Actually no weight should be attached to Terroine and Delpech's material, nor to their conclusion that respiration in fish is independent of size.

All authors, both those that have defended the view that fish metabolism can be described by the surface law, and those who dispute this, have used altogether inadequate material [priemy] on which to base their assertions. As a rule they have used series of experimental data which refer to a narrow [page 90] range of sizes. Under these conditions, in order to come to a reliable conclusion regarding the nature of the relationship between respiration and size it is necessary for the values for oxygen consumption rate to be obtained with utmost accuracy, based upon a large number of measurements, and carried out meticulously under identical conditions. In actuality, not only have these necessary conditions been disregarded, but in general no attention has been given to the inevitable accidental error in the measurements, and no attempts have been made to appraise the reliability of the conclusions drawn. Usually all that has been done is to calculate the rate of oxygen consumption per unit of conventional surface area of the fish, to study the data thus obtained, and to appraise the similarities or differences quite arbitrarily. This applies particularly to Rubner's 1924 data, which can be regarded as conforming to the surface law only by a great stretch of the imagination.

In order to establish any quantitative relationship between phenomena it is necessary to use objective methods in treating experimental data. Only in this way is it possible to get rid of subjectivity and bias in appraising empirical material. Specifically, this is the only way to determine the nature of the relation between rate of metabolism of fish and the total size of the body, or its weight. The studies of the abovementioned authors who endeavoured to solve this problem by unsuitable or inadequate methods can be used, together with many other works, as primary sources of material concerning rate of metabolism of fish of different weights.

2. The method of summarizing quantitative data on the rate of metabolism of fish

The relation of metabolism rate to weight in animals was

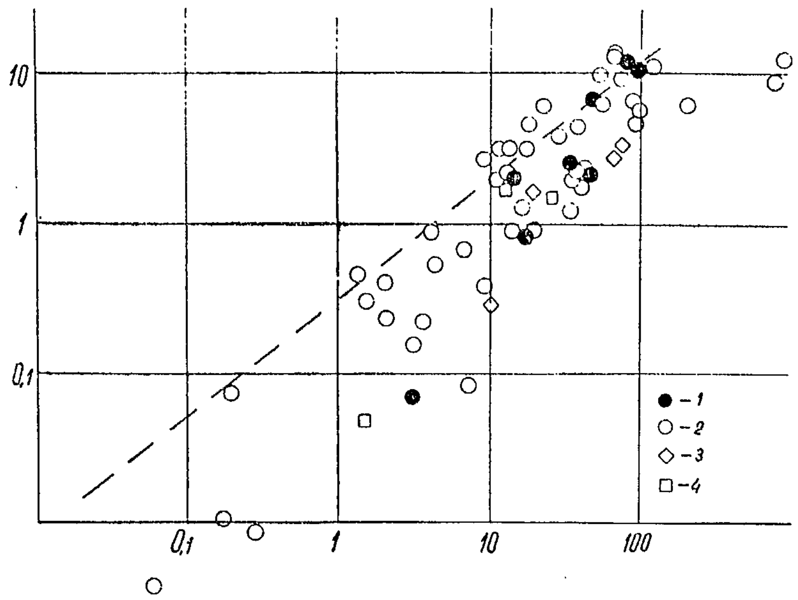

Fig. 27 [page 88]

Relation between total metabolism and size in various marine fishes, from data by Montuori (1907, 1913, 1913a).

Abscissa--weight of the fish in g; ordinate--oxygen consumption in ml per hour, adjusted to 20° (logarithmic scales). 1- eel; 2- other fish, from the data of 1913a; 3- from the data of 1913; 4- from the data of 1907 (see the text, page 88).

first expressed quantitatively for mammals and birds. A similar law has been proposed for crustaceans and insects also (Winberg, 1950, 1956). A suitable method for handling such data has been developed, and fully tested in practice. It has been found repeatedly that the relation of metabolism to size can be expressed quite well by a parabolic equation. However, up to the present no convincing or generally accepted explanation has been offered for this fact. Therefore the parabolic relation between total metabolism and weight has to be considered as an empirical method of summarizing and averaging experimental data.

As is well known, the parabolic relationship of metabolism to weight may be written as:

$$Q = Aw^k$$

where the symbols are as follows:

Q the rate of oxygen consumption [page 91] or some other quantitative index of metabolism of the whole organism, per unit of time (the total metabolism);

A a coefficient equal to the total metabolism of an animal of unit weight;

w the weight of the animal;

k a constant (a pure number) that indicates at what speed and in which direction the metabolic rate changes when weight increases.

In order to compare not the total metabolism, but the rate of metabolism--that is, metabolism per unit weight--with body weight, it is enough to divide both sides of the equation by weight, i.e.:

$$\frac{Q}{w} = Aw^{k-1}$$

If $k = 1$, the [total] metabolism increases in proportion to weight, but the metabolic rate remains constant ($Q/w = A$) and does not depend upon the weight of the animal. When total metabolism increases more slowly than weight, and the metabolic rate is inversely related to the total metabolism, k is less than 1. The more k differs from unity, the more metabolic rate deviates from strict proportionality to weight.

The "surface law" represents a special case of the parabolic relationship. It is satisfied only when $k = 0.67$. In order to establish whether there are any grounds for believing that fish metabolism is proportional to surface one must determine, by objective statistical methods, whether this exponent actually equals 0.67 or differs from this value only by an amount that lies within the range of experimental error. The exponent in the parabolic equation can be estimated with a small degree of error only if the weights of the experimental fish differ greatly. In order to decide whether empirical data are described by a parabolic relationship one must use the logarithmic form, i.e.:

$$\log Q = \log A + k \log w$$

This form of the equation is important because the logarithm of the total metabolism and the logarithm of weight are linearly related. If logarithm of weight is plotted on the abscissa and logarithm of the rate of oxygen consumption on the ordinate, then the empirically obtained points will be located along a straight line if the relation between size and metabolism can actually be represented by a parabola.

When the empirical points on the logarithmic graph are in a straight line, thereby proving that the experimental data can be described by a parabolic relationship, the statistical processing of the material is reduced to a consideration of the linear correlation between log w and log Q and finding [page 92] the parameters of the straight line:

$$\log Q = k \log w + a,$$

where $a = \log A$. This straight line can be regarded as the linear regression of y on x ($y = \log Q$, $x = \log w$). From this point of view, the value of the exponent of weight (k) is the coefficient of regression of y on x.

The simplest method of drawing a straight line--by eye--and a graphical determination of k and a can, with practice, often lead to a satisfactory result. The method of computing the parameters of the equation by least squares is time-consuming but fully objective. Most valuable is the fact that, by this method, it is also possible to determine the statistical error, so that the constants and the reliability of the differences disclosed by the experiment can be judged. The mean square error [standard error] of the exponent (k) is:

$$\sigma_k = \frac{\sigma_y}{\sigma_x}\sqrt{\frac{1-r^2}{n}}$$

where r is the correlation coefficient measuring the closeness of the relation of y to x; in our case, between the logarithm of the rate of oxygen consumption and the logarithm of the weight of the fish.

I have collected all the available results of measurements of fish metabolic rates in order to establish from the totality of the material on hand, rather than from individual pieces of data chosen arbitrarily, how metabolic rates of fish are related to their size (weight).

In collecting and working over the material I have always been guided by the following rules. First of all, I have endeavoured to make use of all available data, i.e. data on fish metabolic rate, which are accompanied by information on the weight of the fish used in the experiments[1]. I have consulted all the research work known to me, published prior to 1954, even if it contains the results of only one measurement, and regardless of the purpose for which it had been done by the author. I departed from this principle only in respect to several works which were definitely unsatisfactory methodologically, containing material which was altogether unreliable and could not be used. This applies to the work of Montuori (1907, 1913) already mentioned, of Terroine and Delpech (1931), and of some other authors (Baldwin, 1923; Pereira, 1924; Spärck, 1932; Kharchenko, 1940; Markova, 1949).

The attempt to make use of all published results of measurements of fish metabolic rates must, of course, [page 93] not be interpreted in the sense that in what follows every measurement of the huge number performed by different authors will be mentioned. This would not only be superfluous but also impossible, if only for the reason that many authors publish only average data obtained from a large number of measurements, although other authors quote the results of individual measurements. In some cases different specimens of fish are used for each measurement; in others, the same specimen is used for successive measurements, etc. All this makes it impossible to include values taken directly from the text, tables or figures of the authors in our summary tables. At times it became necessary to resort to averaging the data of several parallel measurements, or to use mean values of day and night observations, and so forth. Only data obtained under uniform conditions from subjects of about the same weight were averaged. If a study contained material on the rate of metabolism of fish of different species and of different weights, values for the rate of respiration of each weight group of each species have been included in the tables. In cases where the metabolic rate was measured for the purpose of

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[1] Unfortunately many authors who, for one reason or another, have measured rate of oxygen consumption have not published the weights of their experimental animals. This very annoying circumstance greatly restricts the possibilities of using the results of many papers which seem to contain data that would be of great interest had we been informed of the weight of the fish. Without this information a metabolic rate loses most of its value.

experimentally studying the effect of some [external] factor, only the data for the control experiment are included in the tables.

When the original works contained measurements made at different temperatures, the data obtained at 20° or at the temperature closest to 20° have been included in the table. If the mean temperature of the experiments is not stated, but only the range of variation in temperature, the arithmetic mean of the extreme temperatures has been accepted as the average temperature of the measurements. For example, if the temperature ranged from 19 to 21.5° during the measurements, the [average] temperature is taken as 20.25°.

All the values entered in the table were adjusted to a temperature of 20° by means of Table 1 (page 33), which is based on the "normal curve" relationship between metabolism and temperature. Furthermore, the data of all authors--originally expressed in the most varied units of measurement--have been reduced to one form (millilitres of O_2 per gram of weight per hour at 20°).

It is quite clear that the reliability of the values obtained varies greatly. The result of a single measurement, which may not always have been made by a good method, can much more easily deviate from the true value of the rate of respiration of a particular fish than can average data based on numerous careful measurements carried out using reliable methods. This would seem to require assigning different "weights" to different values during statistical processing. However, apart from the inevitable element [page 94] of arbitrariness in estimating a weight for each separate piece of data, other considerations have restrained me from using this method. One must not lose sight of the possibility of systematic error which cannot be eliminated by making a large number of measurements. Furthermore, no increase in quantity of measurements can remove the effect of possible differences in metabolism that depend upon local peculiarities of the material, the conditions under which it was kept prior to the experiment, and so on. For this reason, in order to shed light on the range of the fluctuations in the metabolic rate of the various species, even single measurements made with different material are of value. Their use makes it possible to include data obtained by many authors at different seasons, by different methods, at different geographical localities, and so forth. This consideration impelled me to use all the data included in the tables on an equal basis during statistical processing. This was done in spite of the possibility that some of the tables very likely contain figures that deviate greatly from the true values, and even [mechanical or typographical] errors.

With the method which was adopted for collecting and processing the material the possibility of any kind of conscious bias in selection is excluded, because when the tables were being compiled it was not known what would be the results of the computations made from the material collected in this blindfold fashion. Furthermore, the statistical processing, which could be begun only after the compilation of all the tables, yielded some results that I had never expected.

All the data gathered are presented in Tables 3-16. The tables are constructed uniformly and contain the following columns:

1) reference number;
2) the name of the fish in the same form as given by the authors;
3) the surname of the author, and the year in which the work from which the data were taken was published;
4) the method used in making the determinations;
5) the number of determinations from which average values entered in the columns to follow were obtained;
6) the average temperature at which the measurements were made;
7) the average value of the rate of metabolism expressed in the units used by the authors;
8) the average live weight of the fish used in the experiments, in grams;
9) the rate of metabolism in ml O_2 per gram of live weight per hour, adjusted to 20° by the method of calculation described above (page 33).

In column 4, the most important measuring methods are indicated by the following symbols:

I the sealed vessel method;
II the gas recirculation method;
III the flowing water method;
M manometric methods.

Other methods which do not fit into this classification are explained in the remarks. In column 5 the letter C designates the cases where the value quoted for the metabolic rate is not, in a strict sense, the arithmetic mean of several measurements, but represents one of the values in a regular series of values obtained, for example, when measuring at different [page 95] temperatures, different O_2 pressures, etc. It is evident that in these cases the values for metabolism, which are thus supported by adjacent data, are of considerably greater reliability than the results of individual measurements.

The graphs (Fig. 28-43) are based on the values entered in the last two columns of the tables. In order to establish connection between tables and graphs it will be remembered that logarithms of the weights shown in column 8 are plotted on the abscissa of the graphs, and logarithms of the number of millilitres of O_2 used per hour at 20° by 1 fish of the indicated weight is plotted on the ordinate. Thus in order to obtain the ordinate for one of the points one must take the logarithm of the product of the metabolic rate (column 9) and the weight of the fish (column 8). If necessary, one can easily locate the data from which was obtained each of the 389 values used for the rate of oxygen consumption of the various freshwater and saltwater fishes.

With rare exceptions (carp), the results of the measurements of the respiration of any one species are usually few, and they pertain to an insufficiently broad range of sizes. This precludes our using them as a reliable enough basis for finding the quantitative relationship between metabolism and size. For this reason it is necessary to group the data for various species and to obtain the relation of metabolism to size for fish of different species but belonging to the same family, order, or larger systematic group. In keeping with the radical differences in their ecological conditions, it seems advisable to consider separately the metabolism of marine and freshwater fishes, which as a rule have been studied in different laboratories.

It is remarkable that in all cases the empirical material, when arranged in this way and plotted on a logarithmic grid, produces points that lie along a straight line (Fig. 28-43). This proves that the use of the parabolic equation to express the quantitative relation of total metabolism to body weight is fully justified for fish, as for other animals.

3. The metabolic level of goldfish

The goldfish (Carassius auratus) is a common subject for laboratory work on fish physiology. Many authors, for a variety of reasons, have measured the rate of oxygen consumption of goldfish of different sizes (Table 3, Fig. 28).

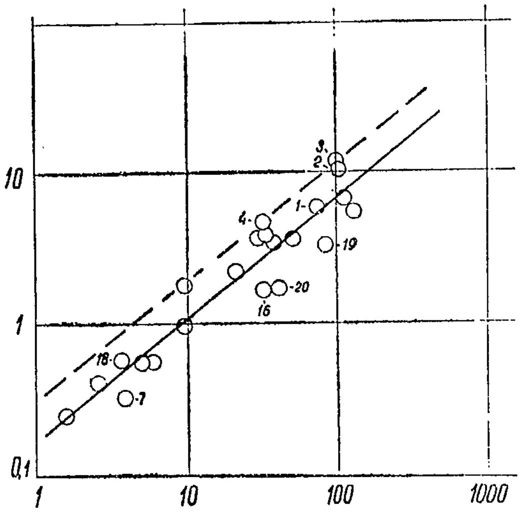

Fig. 28 [page 96]

Relation between total metabolism and body weight in goldfish; from data of various authors (Table 3).

Abscissa--weight of the fish in grams; ordinate--the oxygen consumption of one fish in ml per hour, adjusted to 20°. Logarithmic scales are used. The solid straight line corresponds to equation (5.3.1) and indicates the average level of metabolism of goldfish. The broken line is based on equation (7.3.5), and shows the average level of metabolism for all fish. For the other marks see page 96 of the text, and Table 3.

[page 96] In spite of the fact that data for only one species are shown on Fig. 28, the points have considerable scatter. The vertical distance between the extreme values [at any given fish weight] is as much as 0.5. Since the logarithm of the oxygen consumption rate is plotted on the ordinate, this means that the largest values are about 3 times the smallest (log 3 = 0.477). It is obvious that the reasons for divergence among the results of different measurements can be numerous and diverse. Among them may be included possible differences in the metabolism of different races of the species, differences in physiological condition of the experimental subjects, errors in measurements or in calculations, and many others. Of course, the causes of the disagreement between data of different authors remain unknown in most cases.

All the same, let us take a look at some of the characteristics of the figures representing goldfish respiration. It is noteworthy that the measurements of metabolic rate of goldfish published by Rubner (1924), which were obtained by direct calorimetry, after appropriate conversion (see page 9) yield values which are very close to the average metabolic rate of goldfish found by measuring rate of respiration (Fig. 28, point No. 18).

Of particular interest are the results obtained by Fry and Hart (1948) and Spoor (1946). These Canadian authors, who worked in the same laboratory, were endeavouring to measure the basal metabolism, i.e. the rate of oxygen consumption during complete rest. Fry accepted the minimum oxygen consumption rate observed during a 24-hour day as the value for basal metabolism. [page 98] Spoor, who was studying the influence of degree of activity upon metabolism, had a chance to obtain this value from the results of many measurements of the rate of oxygen consumption at varying degrees of activity (Fig. 45). It can readily be seen in Fig. 28 that points 7 and 16, from the data of these authors, are situated considerably below the straight line representing the average metabolic level for goldfish as computed from all the points. It is true that a few of the measurements of goldfish respiration yield values even less than the "basal metabolism" indicated by the Canadian authors' data. However, this applies only to 3 individual measurements by Bounhiol (1905) and it is unlikely that any importance should be attached to them. The very numerous but (it would seem) methodologically less than perfect measurements of Baudin (1931, 1932) show an exceptionally high level of metabolism for goldfish; this level (points 1-4) being about 3 times as high as the lowest values of Bounhiol or the "basal metabolism" of Fry and Hart, and Spoor.

Like other similar examples, the measurements of goldfish metabolism show how cautious one must be in using measurements of respiration for the quantitative characterization of the metabolic rate of any species. For this purpose it is not advisable to limit oneself--though this has often been done--to any single series of measurements, however extensive it may be. Rather, all the available material should be studied. In the case of goldfish, regardless of the considerable scatter of the points, the correlation coefficient between log Q and log w is high ($r = 0.948$), indicating a rather close relationship between these quantities. The regression equation found by least squares is:

$$y = 0.81\,x - 0.759$$

whence:

$$Q = 0.174\,w^{0.81} \tag{5.3.1}$$

From this we can find, for a goldfish of any given weight, the expected value of the metabolic rate corresponding to the average for all the measurements. As examples, we will determine to what extent the values of basal metabolism obtained by Fry and Hart for a fish weighing 3.8 g, and by Spoor for a fish weighing 32 g, deviate from the average.

In the former instance the expected total metabolism for a fish weighing 3.8 g, according to equation (5.3.1), is:

$$Q = 0.174 \times 3.8^{0.81} = 0.174 \times 2.95 = 0.513$$

Hence the rate of metabolism is:

$$\left(\frac{Q}{w}\right) = 0.135\left[\text{ml } O_2/\text{g/hour at } 20^\circ\right]$$

[page 99] In a similar way we obtain the following for the second example:

$$\frac{Q}{w} = 0.090 \text{ ml } O_2/\text{g/hour at } 20^\circ$$

The observed level of basal metabolism in the first example was 0.085 ml O_2/g/hour at 20°, and in the second it was 0.054 (Table 3, Nos. 7 and 16), i.e. the basal metabolism was respectively 63% and 60% of the expected average metabolic rate. The close correspondence of the last two values, calculated from the data of different authors and from fish of different weights, appears to indicate that goldfish metabolic rates given by equation (5.3.1) are about 60% higher than the basal metabolism.

In what follows we shall see that the value obtained for the exponent ($k = 0.81$) must be regarded as a very probable one, when compared with data for other species. Nevertheless, within the limits of the total data for goldfish, it cannot be considered as proven that the estimated value of k is actually close to the true value, because of the small number of points ($n = 22$). In spite of the relatively large correlation coefficient, the standard error of k is large ($\sigma_k = 0.060$, or 7.5% of k). Using the usual criterion for testing the reliability of differences, the deviation of the observed value of k from the true value can be $\pm 3\sigma_k = \pm 0.18$.

This example shows that the value k can be computed with an adequate degree of accuracy only if there is available a considerable body of primary data representing a wide range of weights. Therefore, in spite of the large number of measurements made of the rate of oxygen consumption, it is not yet possible to obtain values of A and k for each species of fish individually. This does not apply to carp, for which data are available over a wide range of weights.

Anticipating some remarks to follow, we may point out that it is possible, by using all the available data, to obtain an equation that represents the average level of metabolism for all the fish that have been studied. On Fig. 28, and on all subsequent graphs, this average level of metabolism for all fish is shown by a broken straight line. The position of the points on Fig. 28 shows plainly that goldfish have a lower metabolic rate than the average for all fish, which is quite natural for an aquarium fish.

4. The metabolic level of carp [page 100]

To illustrate the relation between metabolic rate and weight within a single species, the measurements of respiration in carp are very important. With this species it is possible to compare the respiration of fish that differ widely in weight, from a few milligrams up to several kilograms (Table 4, Fig. 29).

In spite of the different methods and conditions of measurement used by different authors, and a very wide range in weight, all the points on the logarithmic graph are located along a straight line, with very little scatter. In keeping with this, the correlation coefficient is very high ($r = 0.997$), so that it is possible to compute k with a considerable degree of reliability. For carp:

$$k = 0.85 \pm 0.012; \qquad Q = 0.343\, W^{0.85} \qquad (5.4.1)$$

[page 103] It is very interesting to observe the contrast between the greatly scattered distribution of the goldfish data, shown earlier, and the unexpectedly good alignment of the figures describing the metabolism of carp, in spite of the fact that both cases involve measurements made by many authors, in different countries, at different temperatures, by different methods, etc. It is difficult to say whether this is an indication of a more heterogeneous "racial" composition of the goldfish used in the experiments, or the result of greater differences in the conditions for growth and development of an aquarium-reared fish in comparison with the pond-reared carp.

G. G. Winberg and L. E. Khartova (1953) made a special study of the rate of oxygen consumption of young carp from the moment of hatching until they had attained an age of 42 days. From 129 separate observations (Fig. 30) the value of k was computed, which in this case equalled 0.98. In other words, it was found that in spite of the considerable range of weights studied (from 2.0 mg to 3.8 g), the rate of metabolism changed only slightly with weight; it remained almost constant over the entire range studied. It is hard to say what caused so unexpected and completely unprecedented a result[1]. We can only point out that in endeavouring to describe the metabolism of young carp under conditions close to the natural, Winberg and Khartova used fry that had been captured from the pond immediately prior to their experiments, and during the time of the experiments the jars were submerged in the water of the pond. Thus all the measurements were made with material that had been growing under natural conditions, and at a temperature and lighting that were very close to natural.

As a result of the unexpected results of the measurements just described, made in 1951, a series of aquarium tests with young of Amur wild carp was performed during the next season. It was found that among these fish, which were reared in an aquarium, the rate of metabolism of fry exhibited an extremely sharp inverse relationship to size. The value of k was very small. Such a radical difference between results of aquarium experiments and observations on metabolism of fry grown under natural conditions is very instructive, even apart from its cause. This example leads to a conclusion of considerable theoretical importance. It is evident that in one and the same species the magnitude of the relation of metabolism to weight can depend largely on the conditions under which growth takes place. Therefore, in intraspecies comparisons at least, the weight exponent (k) can differ significantly under different growing conditions.

[page 104] We might expect from general considerations that under conditions of poor growth metabolic rate should decrease especially rapidly with increase in weight. The most

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[1] In the report written concerning these experiments, attention was called to these unexpected results, but this section was deleted by the editors of "Doklady AN SSSR".

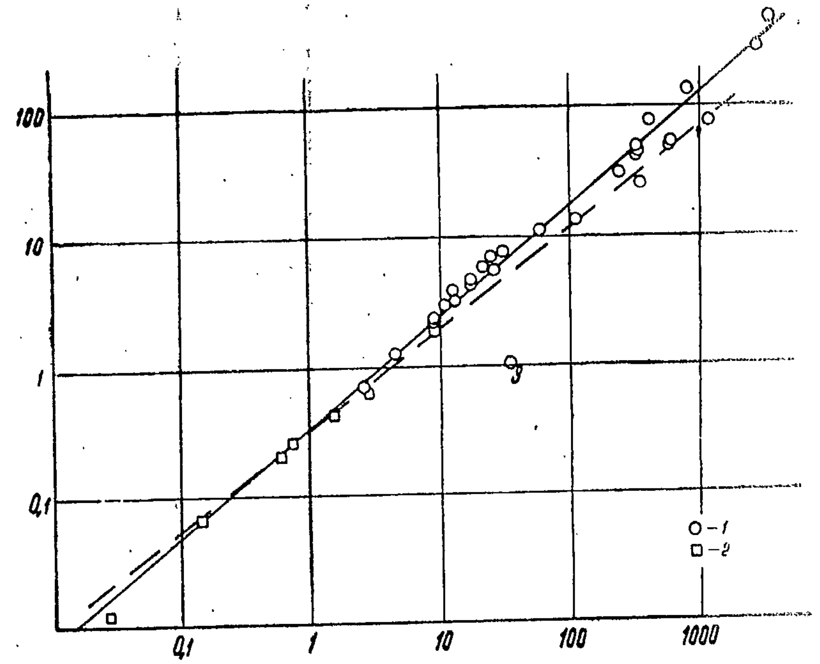

Fig. 29 [page 100]

Relation between total metabolism and body weight in carp, from data of various authors (Table 4). Axes as in Fig. 28.

The solid straight line, drawn according to equation (5.4.1), shows the average metabolic level of carp; the broken line, as in Fig. 27, 28, 31-39 and 41-44, is based on the equation (7.3.5) and shows the average level of metabolism for all fish. 1- pond carp; 2- young wild carp, from Krivobok's data; 3- Ivlev's data obtained using fish in poor condition.

favourable conditions, it would seem, should produce the reverse effect. Under optimal growth conditions the slowest reduction in the metabolic rate with increasing size should be expected, i.e. high values of k, approaching unity.

Nevertheless, it would be premature to say that it has been proven that Winberg and Khartova's results are typical of natural conditions. It may be that the almost complete independence of metabolic rate and weight in these young fish represents, in part possibly, an effect of errors in method that were not taken into account. For example, it can be assumed that the respiration of the smallest fish did not increase when they were placed in the respiration vessel, while in young fish of larger size this phenomenon could be much more in evidence. [page 105] Possibly this could explain the fact that the respiration rate of the smallest fish, according to Winberg and Khartova's data, does not differ from the rate expected from equation (5.4.1) based on the data in Table 4, whereas the respiration of the larger fingerlings was considerably greater than expected, so that the net result was that respiration appeared to be independent of body size in these small fish. However that may be, it is worth while to emphasize once again that the changes in metabolic rate which accompany growth and development of fish are complex in nature. They depend on many factors, which are not as simply and definitely related to size and stage of development as is sometimes supposed.

The results of 44 measurements of the rate of oxygen consumption of verkhovka are also shown in Fig. 30 (8 measurements on fish of 20-40 mg, 36 on fish of 140-960 mg). It is very interesting that the data do not show any differences from the respiration rate of young carp of corresponding weight.

The data under discussion concerning the metabolism of goldfish and carp are of interest in the sense that they pertain to age differences in size[1] within each of these two species. In both cases the aggregate of all data on hand points to a decrease in respiration rate with increase in weight; however it is a considerably slower decrease than would be expected from the surface law (k = 0.67).

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[1] [see p. ~~XXX~~ 72 of the translation for a discussion of this expression.]

Chapter VI. [page 106]

Metabolic Rate and Total Body Size in Fish (continued)

1. The metabolic level among various freshwater fishes

A large number of measurements of the oxygen consumption rate over a wide range of weights has accumulated in the literature with respect to sturgeons. However, here as in subsequent cases, it is material in which within-species age differences of size are mixed with differences between species (Table 5, Fig. 31).

Figure 31 shows that here too the data plotted on the logarithmic graph are well described by a straight line; and what is especially important, the measurements include a very wide range of weights (6 orders of magnitude). The greatest weight (10.4 kg) is 450,000 times the smallest weight (23 mg).

In keeping with the small scatter of the points, the coefficient of correlation is equal to 0.997 and k can be determined with great accuracy. For sturgeons:

$$k = 0.81 \pm 0.010; \qquad Q = 0.391\, w^{0.81} \qquad (6.1.1)$$

It is noteworthy that in the present example there is excellent agreement with the general law of change in metabolism with size, both for differences within a single age-group--for example, young osëtr and sevriuga--and also for the metabolism of grown-up sturgeons of different species and sizes.

Thus any species differences in metabolic rate are concealed by the differences between the metabolic rates of fish of different sizes. Furthermore, the level of metabolism characteristic of each of these species is not rigidly fixed, rather it depends to a considerable extent upon associated conditions, which further complicates the task of determining species differences in level of metabolism.

The data for salmonoid fishes are collected in Table 6 and in Fig. 32. Here the points on the graph are much more scattered, possibly because of the great mobility and excitability of these [page 107] fish, which makes it more difficult to obtain data on resting metabolism. Nevertheless the correlation coefficient is still high ($r = 0.976$).

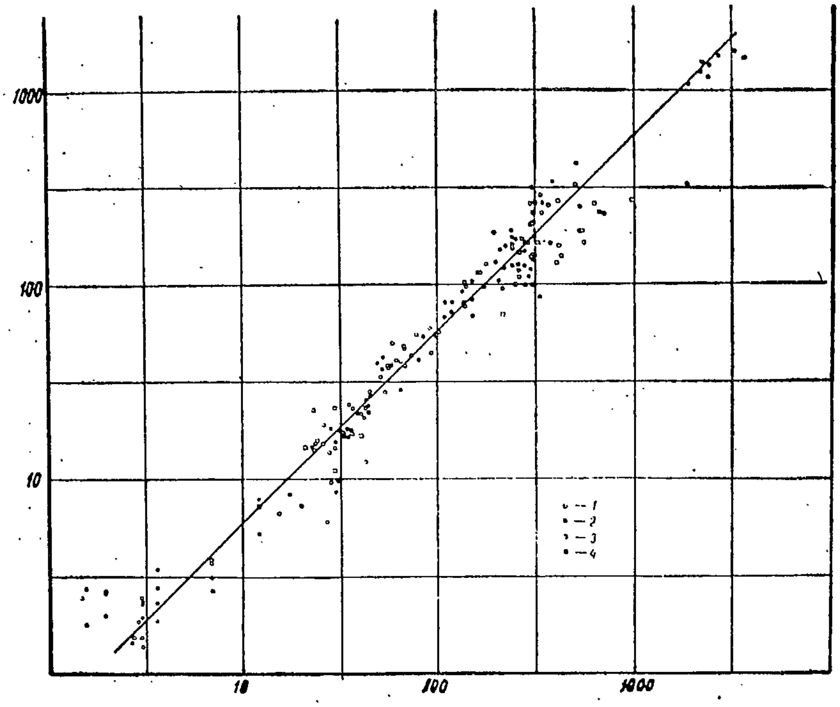

Fig. 30 [page 104]

Relation between total metabolism and body weight of young carp and verkhovka, from data of Winberg and Khartova (1953). The general construction of the graph is as in Fig. 28.

1 and 2- young carp; 3 and 4- young verkhovka. 1 and 3- measurements made in daylight; 2 and 4- measurements made in the dark. The straight line shows the average metabolic level for young carp (see the text, page 104). This graph is on a larger scale than Fig. 27, 28, 31-39 and 41-44. [The abscissa is in milligrams, and the ordinate in ml$\times 10^{-3}$/fish/hour, at 20°.]

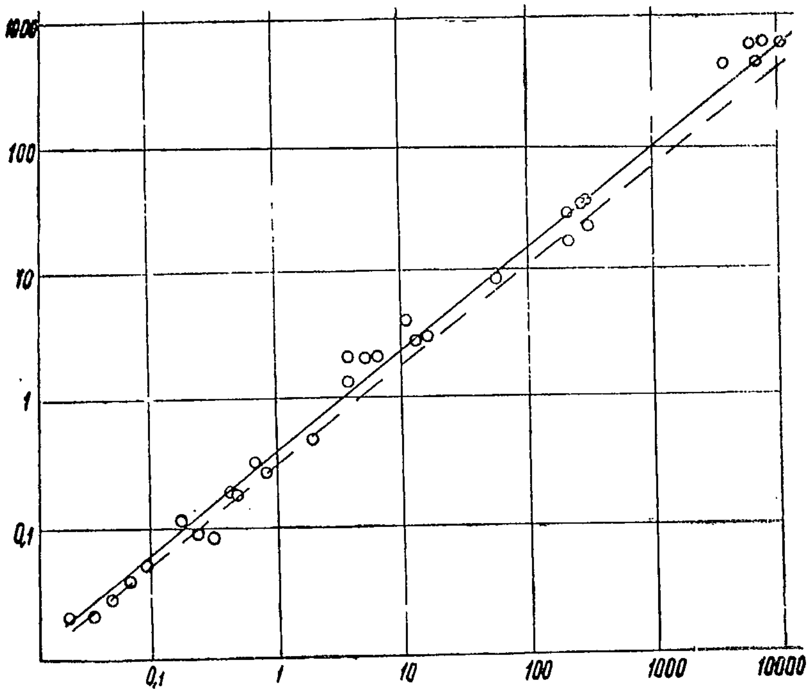

Fig. 31 [page 107]

Relation between total metabolism and body weight in sturgeons, from data of various authors (Table 6). Axes as in Fig. 28.

The solid straight line is based on equation (6.1.2); the broken line indicates the average level of metabolism for all fish (equation 7.3.5).

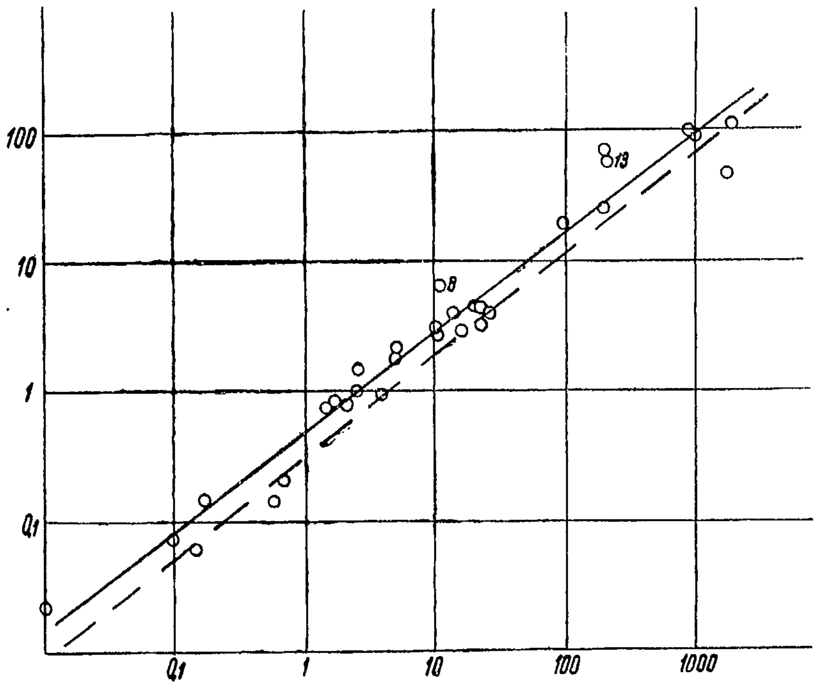

Fig. 32 [page 112]

Relation between total metabolism and body weight in salmonoid fishes, from data of various authors (Table 6). Axes as in Fig. 28.

The solid straight line corresponds to equation (6.1.2); the broken line is the average metabolic level for all fish.

$$k = 0.76 \pm 0.032; \qquad Q = 0.498\, w^{0.76} \qquad (6.1.2)$$

As for the sturgeons, this equation is based upon data that refer to the metabolism of "adult" [vzroslye] fish of various sizes and also young fish in different stages of growth [u malkov raznykh vozrastnykh stadiĭ].

Among the various materials on salmonoid fishes, one figure is of particular interest (No. 3, Table 6) because it was obtained from specially careful measurements of the "basal metabolism", i.e. of the minimum rate of metabolism observed during 24 hours of observation. For fish of the corresponding weight (23.25 g) we obtain from equation (6.1.2) an expected figure for metabolic rate of 0.239. The experimentally determined figure for the basal metabolism of Salvelinus fontinalis is 0.140, or 58.6% [page 112] of the expected. It is interesting that, in agreement with what was found for a species with a different level of metabolism (goldfish, page 98), the basal metabolism in this case also was about 60% of what was expected from the average of the results of measurements on the metabolism of these fishes (see also page 184).

Very interesting also are the data of V. S. and I. V. Ivlev (1952), who measured the metabolic rate of young salmon (Salmo salar) of different sizes and weights (0.87 to 40.1 g). On the basis of 36 measurements they found that here too the relation of metabolic rate to weight can be expressed by a parabolic equation. The exponent of weight, determined graphically, was 0.81.

[page 113] The value of a corresponding to these data is equal to about 0.40 ml O_2 per g per hour at 18-20°. Thus, according to this material--which was not used in obtaining the equation (6.1.2)--the value of Q for salmon fingerlings is equal to $0.40w^{0.81}$. This is very close to the equation obtained above, characterizing the metabolism of all salmonoid fishes (6.1.2). The difference of 0.05 between the exponents of the independent variable is within the limits of random error, since:

$$\sigma_k = \pm 0.03$$

On the other hand, according to T. I. Privolnev's data (1953, table 1) for the same species, which pertain to a rather small range of weights, a greater dependence of metabolism on body size is observed, corresponding approximately to $k = 0.67$. These latter data apply to fish grown in ponds. It is quite possible that in this case the reduction in the metabolic rate is related not only to increase in size but that it also reflects the process of adaptation to pond conditions, which was accompanied by lowering of the metabolic rate (page 65).

The material on all the freshwater cypriniform fishes, except the goldfish and carp studied above, is collected into Tables 7 and 8 and shown in Fig. 33 and 34. Here we encounter a large [page 114] number of different fish species, and a smaller range of sizes for which data on metabolic rate are available. Accordingly it is impossible to estimate sufficiently accurately the values of a and k for separate species. Nevertheless, in view of the fact that the available measurements for respiration of tench seem to indicate a lower metabolic rate in this species, they were calculated and are depicted separately. For tench we get:

$$k = 0.79 \pm 0.051; \qquad Q = 0.230\, W^{0.79} \qquad (6.1.3)$$

[page 122] For all the freshwater cyprinid fish with the exception of goldfish, carp and tench:

$$k = 0.80 \pm 0.044; \qquad Q = 0.336\, W^{0.80} \qquad (6.1.4)$$

For the other freshwater fishes, we will limit ourselves to a graphical presentation of the available data, which are not sufficient to calculate reliable values of a and k. However, Fig. 35-38 show convincingly that among lampreys, eels, perch and other freshwater perciform fishes, and pike, neither the average metabolic level nor the numerical relationship between metabolism and weight differ appreciably from the average metabolic level for all fish, which is shown in these figures by a broken straight line. We might notice just one thing, that from the available data (Fig. 36) the eel has a metabolic rate somewhat lower than average (about 70-75% of the mean for all fish). It is not impossible [page 123] that this is a result of difficulties encountered in measuring metabolism in this fish.

The data on the respiration of lampreys (Fig. 35) and pike (Fig. 38) agree well with the average for all fish. In the same way, among the freshwater perciform fishes (Fig. 37) only measurements made on the North American representatives of this order (Table 11, Nos. 15, 16, 19, 20) deviate appreciably from average metabolism.

The small viviparous aquarium fishes belonging to the order Cyprinodontiformes comprise a separate group. It is very interesting to determine a mean metabolic level characteristic of this group; for its representatives, after reaching maturity, do not exceed the 1½- to 2-month-old young of many freshwater fishes in size. The measurements (Fig. 39) all agree in showing that the metabolic rate of these small fish is somewhat lower than the mean rate for other fish of corresponding sizes. It is significant that this applies not only to the mature fish but also to the young. According to data on hand, $k = 0.71 \pm 0.042$, indicating a greater change in

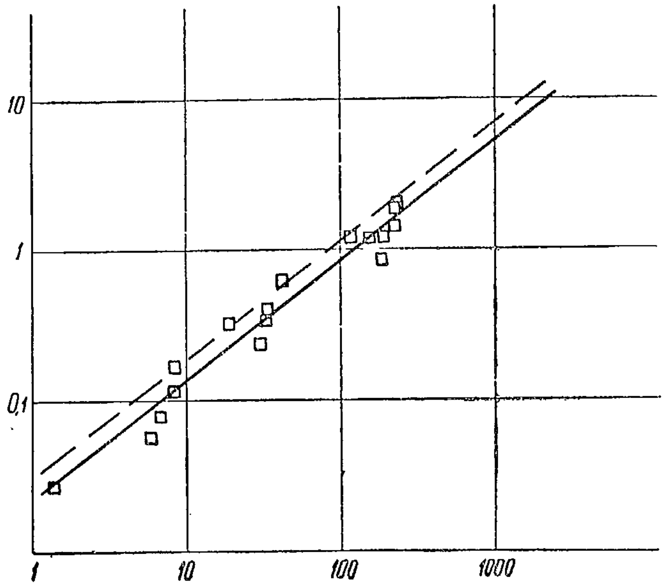

Fig. 33 [page 113]

Relation between total metabolism and body weight of tench (Table 7). Axes as in Fig. 28.

The solid straight line is based on equation (6.1.3); the broken line shows the mean level of metabolism for all fish (equation 7.3.5).

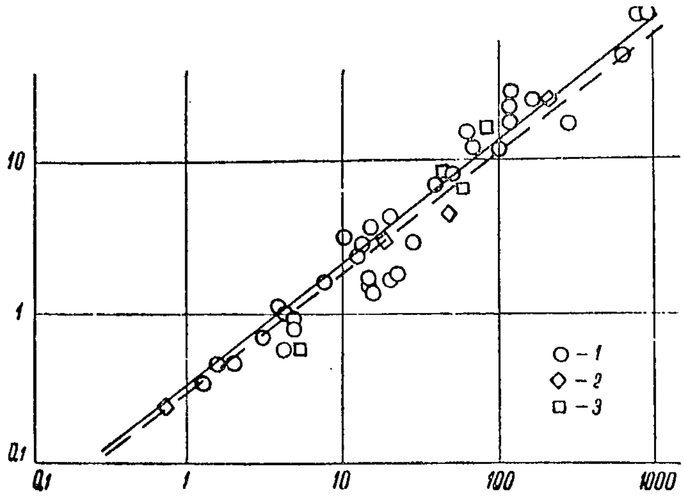

Fig. 34 [page 114]

Relation between total metabolism and body weight of freshwater cypriniform fishes, from data of various authors (Table 8). Axes as in Fig. 28.

The solid straight line is from equation (6.1.4); the broken line shows the average metabolic level for all fish (equation 7.3.5). 1- freshwater cyprinid fishes; 2- other freshwater cypriniform fishes; 3- crucian carp. The data for roach (Table 8, Nos. 36-44) are not shown.

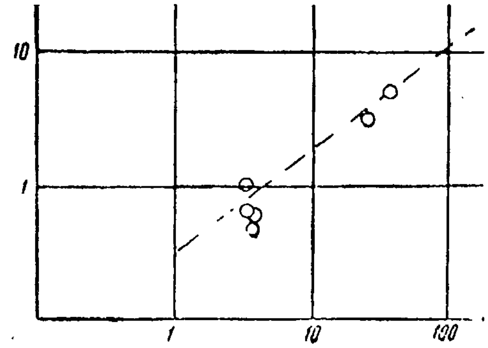

Fig. 35 [page 114]

Relation between total metabolism and body weight in lampreys, from data in Table 9. Axes as in Fig. 28.

The broken line is the average metabolic level for all fish (equation 7.3.5).

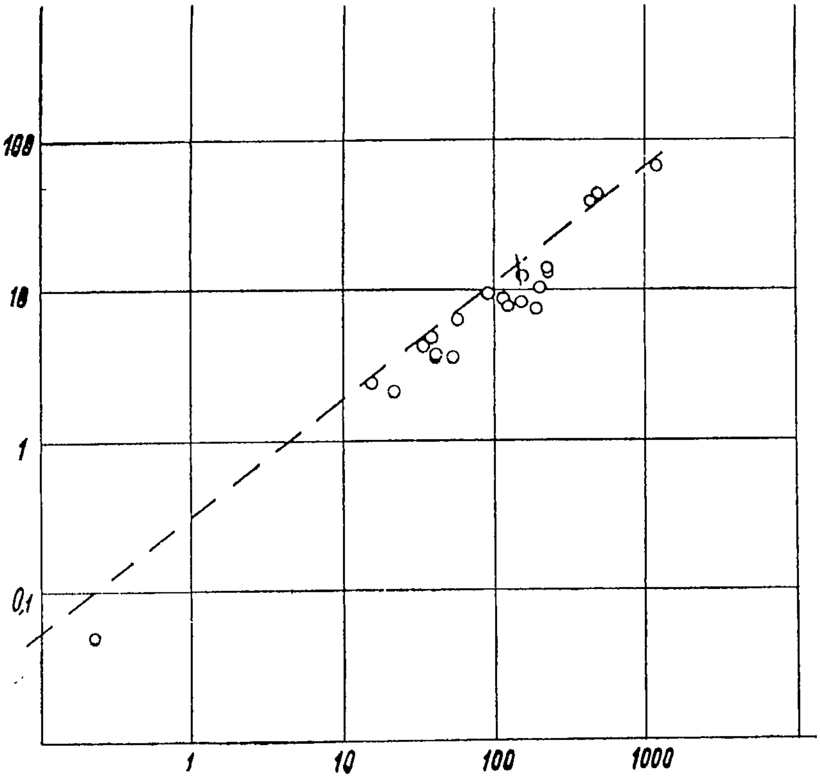

Fig. 36 [page 122]

Relation between total metabolism and body weight in the eel, from data of various authors (Table 10). Axes as in Fig. 28.

The broken line is the average metabolic level for all fish (equation 7.3.5).

metabolism with size than in the examples collected above. However, the large size of the standard error will not permit us to regard this difference as strictly proven. It is interesting that the metabolic level of the viviparous fishes ($a = 0.192$) is only slightly below that expected for fish [generally] at a corresponding weight, and the rate for the goldfish is even lower.

In this instance it is not clear whether the lowered metabolic level in these fish can be linked with the fact that they are kept in aquaria, seeing that I. Kh. Maksudov (1940, 1948), who made a special study of the relation [page 124] between respiration and size in Gambusia affinis holbrooki, used material that was captured in nature. However, prior to the experiments he kept his fish for several days without food. This is quite a long time for such active fish at temperatures of 20-32°. Furthermore, it is hard to know how well conditions along the Caucasian coast meet the requirements of this species, which has just recently been acclimatized in that locality.

Maksudov (1940), after completing a considerable number of measurements (74) of the rate of oxygen consumption and release of ammonia gas by Gambusia of 6 weight groups (0.23-1.37 g) expressed the relation of metabolism to weight by means of a hyperbola. The oxygen consumption (R), according to this author, is related to the weight of the fish as follows:

$$R = \frac{1}{0.924 + 0.009w}$$

where: R is oxygen consumption in mg O_2 per hour per unit weight (in centigrams)

w is weight of the fish in centigrams.

The release of ammonia gas (U) is related to weight in the following manner by Maksudov:

$$U = \frac{1}{13.45 - 0.18w}$$

where: U is the ammonia released, in mg NH_3 per hour per unit of weight (in centigrams).

Maksudov is not at all disposed to argue that an hyperbola is the most suitable form of expression for his data; rather, he also furnishes computations which show that the quotient obtained by dividing the amount of oxygen absorbed by $w^{2/3}$, in his opinion, is constant (0.024-0.029). If actually, as he assumes, the total respiration of Gambusia changes in proportion to the conventional estimate of surface ($w^{2/3}$), then there exists a parabolic rather than a hyperbolic relation between w and R, for which:

$$\frac{R}{w^{0.67}} = \text{constant}$$

[page 126] However, because the weight range (0.23-1.37 g) is so limited, the extreme quantities differing only by a factor of 6, there is not much use in discussing which formula best expresses the results obtained. Therefore there is no reason to refrain from applying to these data also, the parabolic type of equation which has been justified in so many cases. Taking into consideration the number of measurements in each of the weight groups, we obtain k = 0.63 from Maksudov's material. Therefore metabolism is unusually dependent on size, even more than would be expected from the surface law. The data contained in the second work of the same author (1948) lead to the same value of k. Of the 25 values in Table 13, 10 were taken from the works of Maksudov. This has led to a value of k for the entire group of viviparous fish that is lower than most:

$$k = 0.71 \pm 0.042$$

For all the Cyprinodontiformes that were studied:

$$Q = 0.192 w^{0.71} \qquad (6.1.5)$$

The materials concerning respiration of different groups of freshwater fishes exhibit a number of differences, whose significance will be discussed later. However, it is already apparent that these differences are not so great that it would be useless, employing the entire material of Tables 3-13, to obtain an equation that reflects the average metabolic level in its relation to weight for all freshwater fishes. The data used concerning respiration of freshwater fishes, including those for goldfish and carp, comprise [page 127] 266 pairs of values. Many of these represent means of numerous measurements.

For all freshwater fishes:

$$k = 0.81 \pm 0.014; \qquad Q = 0.297\, w^{0.81} \qquad (6.1.6)$$

As a confirmation of expression (6.1.6), which generalizes a large number of measurements by various authors, the results of the important study by V. S. Ivlev, published just recently, are of exceptional importance (1954). Ivlev measured the rate of oxygen consumption of freshwater fishes belonging to 22 species, at 18-20°. In addition to a number of cypriniform fishes, these included the brook lamprey, sterlet, eel,

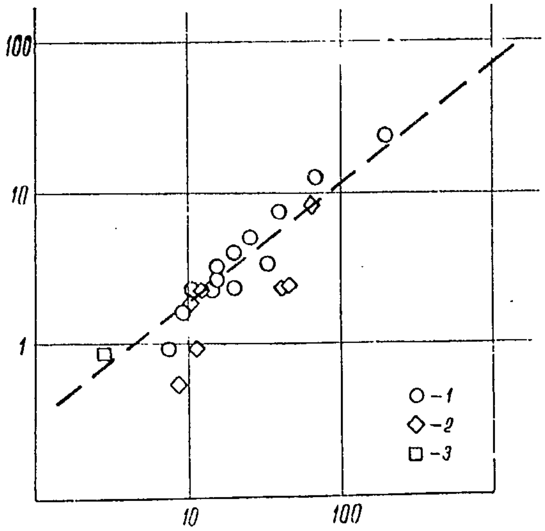

Fig. 37 [page 123]

Relation between total metabolism and body weight in perciform fishes (Table 11). Axes as in Fig. 28.

The broken line is the average metabolic level for all fish. 1- perch; 2- other freshwater Percidae; 3- sculpin.

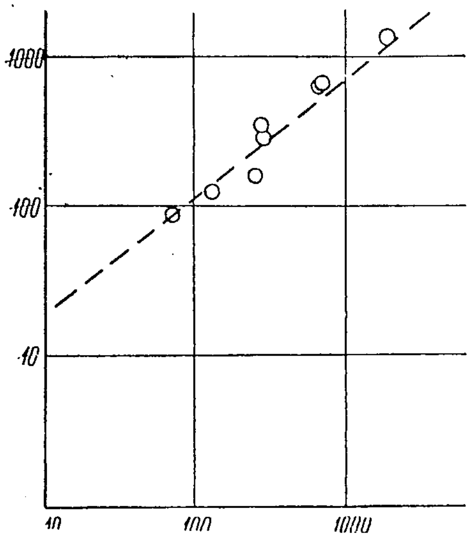

Fig. 38 [page 124]

Relation between total metabolism and body weight in pike (Table 12). Axes as in Fig. 28.

The broken line is the average metabolic level for all fish (equation 7.3.5).

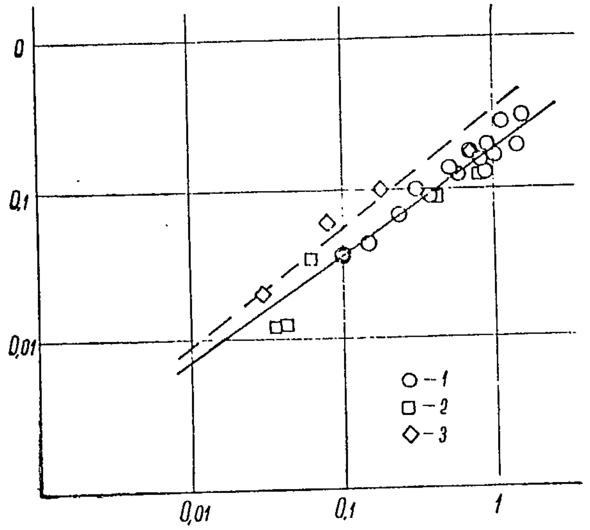

Fig. 39 [page 126]

Relation between total metabolism and body weight of freshwater Cyprinodontiformes (Table 13). Axes as in Fig. 28.

The solid straight line is based on equation (6.1.5); the broken line is the average metabolic level for all fish (equation 7.3.5). 1- Gambusia; 2- Girardinus; 3- guppy.

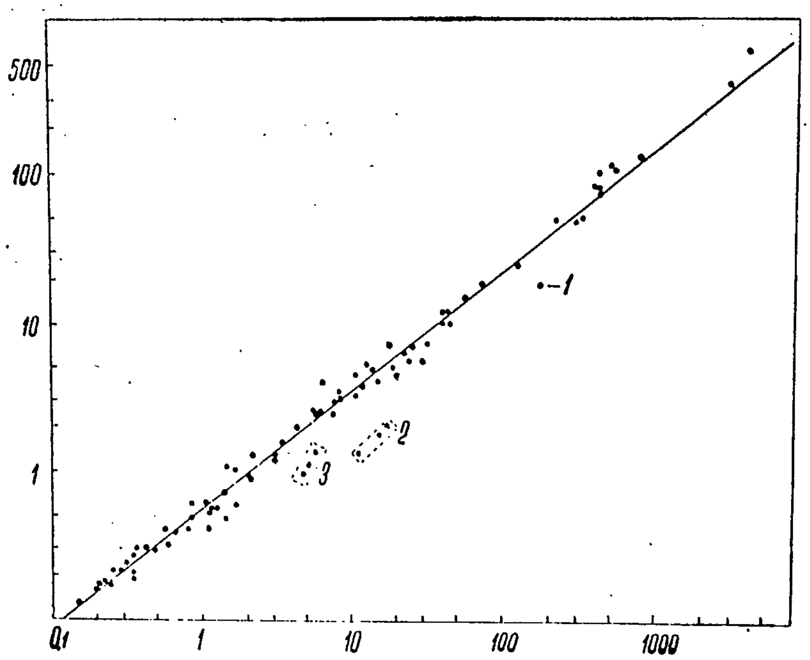

Fig. 40 [page 127]

Relation between the total metabolism and body weight in various freshwater fishes, from V. S. Ivlev (1954).

Abscissa--body weight in grams; ordinate--the oxygen consumption in mg per hour at 18-20°. 1- eel; 2- stone loach; 3- lamprey (see text, page 127).

ninespine stickleback, salmon (36 measurements, page 112), trout, pike and perch. Of special value is the fact that Ivlev's measurements embrace a wide range of weights of the fish used in his experiments (from 0.2 to 3487 g).

From his data Ivlev came to the conclusion that the relation of metabolism of fish to body weight follows [page 128] a parabolic relationship nicely. On the logarithmic graph on which the results of all his 82 measurements are shown (Fig. 40), a majority of points are situated close to the straight line. Only the 3 measurements of lamprey respiration, 3 of the 4 measurements of respiration for stone loach, and 1 of the 2 measurements for the eel deviate towards a lower metabolic rate.

Fitting a straight line graphically by eye, Ivlev finds the equation of the parabola which describes his data. In the form adopted by us it is:

$$Q = 0.39\ w^{0.81}$$

It is noteworthy that Ivlev quite independently, from his own measurements, has arrived at the same exponent of weight as we had obtained for all freshwater fishes (6.1.6). When independent data coincide it speaks well for their reliability.

The proportionality coefficients (a) differ somewhat. However, here too the difference is small. When drawing his straight line V. S. Ivlev failed to consider the divergent points for lamprey, stone loach and eel. It can be seen from the figure that if all points were to be considered, as I did without fail in obtaining the parameters of equations by the least squares, then the quantity a would be closer to 0.3. Therefore Ivlev's data can serve as a solid confirmation of the fact that equation (6.1.6) is an accurate description of the relation between the mean value of the metabolism and body weight in freshwater fishes.

2. The metabolic level of marine fishes

The available data on respiration of marine fish are less numerous and somewhat different from those for freshwater fish.

Here we do not find any material that can be used to demonstrate the nature of the relation between metabolism and size within a single species. It is also difficult, in view of the great variety of marine fishes, to group the results of measurements according to their systematic classification, as was done for freshwater fishes. It is convenient to consider first the extensive material gathered by Jolyet and Regnard

(1877) and, especially, by Bounhiol (1905). The latter continued the research of Jolyet and Regnard, working at the same place (Concarneau, on the English Channel) and using the same methods. All the values obtained by these authors are compiled in Table 14 and depicted in Fig. 41. In spite of the method of these authors, which did not exclude the possibility that the fish could move, so that there could be great differences in rate of [page 129] oxygen consumption between slow-moving and active fish, the scatter of the points is slight and the correlation coefficient between y and x is quite high ($r = 0.968$). According to these authors' data, obtained for fish of the most varied systematic position,

$$k = 0.87 \pm 0.32; \qquad Q = 0.266w^{0.87} \qquad (6.2.1)$$

The slightly higher magnitude of k may be related to the use of a gas recirculation respiration apparatus, in which the fish were able to move about. This could have increased the metabolism of the larger fish relatively [to the smaller ones].

The data of other authors, pertaining to a varied assortment of marine teleosts, obtained by different methods and at different geographical points (Table 15, Fig. 42), naturally exhibit great divergences. But here too the correlation coefficient is fairly high ($r = 0.882$). According to these data:

$$k = 0.80 \pm 0.072; \qquad Q = 0.224w^{0.80} \qquad (6.2.2)$$

The scanty data on respiration of elasmobranchs, in view of their radically different systematic position, have been grouped separately (Table 16, Fig. 43). The graph shows plainly that in this case too the distribution of the points is well described by the straight line based on the mean data for all fishes. Of the 10 values that were used for constructing the figure, 5 were taken from the work of Buytendijk (1910), who measured the oxygen consumption of the sharks Scyllium cassicula and S. canicula at various sizes, in an endeavour to determine the relation between respiration and size in fish. Although his measurements are insufficient to obtain reliable values of a and k, it is interesting that the value k computed from his data is 0.80.

[page 134] The above material does not include any measurements of respiration of fry or fingerlings of marine fishes. Hence the results of Zeuthen are of some interest in this respect, though unfortunately they are presented only in the form of a graph (Zeuthen, 1947, fig. 32, 40). These measurements pertain to the young of various saltwater fishes belonging to Clupeini, Pleuronectidae, Syngnathidae and others. Reading the coordinates for all the 25 points from Zeuthen's figure 40, adjusting the values so obtained to 20°, and

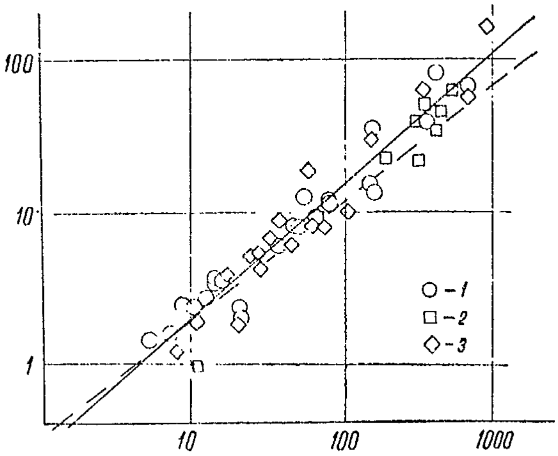

Fig. 41 [page 129]

Relation between total metabolism and body weight in various marine fishes, according to Jolyet and Regnard (1877) and Bounhiol (1905) (Table 14). Axes as in Fig. 28.

The solid straight line is based on equation (6.2.1). The broken line describes the mean metabolic level for all fish (equation 7.3.5). 1 and 3- data of Bounhiol; 2- data of Jolyet and egnard.

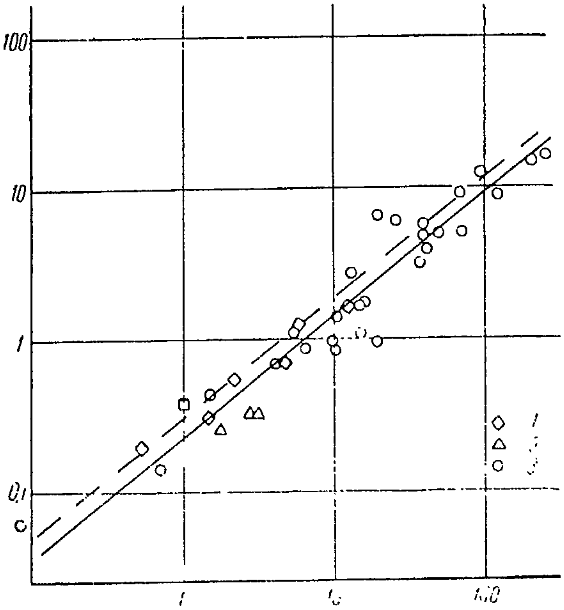

Fig. 42 [page 134]

Relation between total metabolism and body weight in various marine fishes, from data by various authors (Table 15). Axes as in Fig. 28.

The solid straight line is based on equation (6.2.2); the broken line is the average metabolic level for all fish (equation 7.3.5).

treating them in the usual way, we obtain:

$$k = 0.71 \pm 0.067; \qquad Q = 0.328w^{0.71} \qquad (6.2.3)$$

In this case there is a considerable change in respiration [rate] with weight. However because of the great scatter of the points ($r = 0.907$) and their small number, the error in k is large. There is very little likelihood that the difference from the mean value of k, 0.8, is real. The level of respiration is high in these data. This may be due to the fact that Zeuthen measured freshly caught material.

The work of Scholander (1953) contains important material on the relation of respiration to size for 7 species of tropical, primarily marine, fishes (Fig. 19).

[page 136] From these data, which are presented only in the form of a chart, it can be seen that k is close to 0.85, as the author himself points out. The value of a at 30° is approximately 0.36. If the adjustment we have used is applied, then at 20° a = 0.160. Hence, according to Scholander's data

$$Q = 0.160w^{0.85}$$

Scholander's measurements are interesting because, in contrast to most other data, they pertain to tropical fish. It is pertinent that he obtained for them the lowest known value for a, 0.160. This nicely confirms Scholander's belief in a lower metabolic rate among tropical fishes (page 50).

From the entire material for marine fishes, which includes 123 values, we obtain:

$$k = 0.79 \pm 0.014; \qquad Q = 0.321w^{0.79} \qquad (6.2.4)$$

3. Comparison of the metabolic levels of fishes of different systematic positions

[page 137]

After comparing metabolic levels of fish of different taxonomic groups and species, let us define the meaning of the term "level of metabolism" [uroven obmena], which must not be confused with rate of metabolism [intensivnost obmena]. At any constant level of metabolism for a given subject, the metabolic rate can vary, in relation to temperature or body size, 10-fold, 20-fold or more. Only if the other conditions are the same is it possible to estimate the level of metabolism from the metabolic rate. Since the total metabolism [obshchiĭ obmen] and the metabolic rate are connected through the weight of the body of the fish, i.e. they conform to an established law, the metabolic level characteristic of a species or a group of species can be stated only by means of an expression which relates metabolism to size. The parabolic equation given above can be used for this purpose. When this method of summarizing data is used, the metabolic level is characterized by two parameters--the exponent of weight (k), and the proportionality coefficient (a). For example, it was found for carp above that $Q = 0.343w^{0.85}$, whereas for salmonoid fishes $Q = 0.498w^{0.76}$. This means that a carp weighing 1 g at 20° consumes 0.343 ml O_2 per hour, but a salmonoid fish of the same weight consumes 0.498 ml O_2, that is, at a weight of 1 g salmonoid fish have a considerably greater metabolic rate than carp. However, if we compare the rate of oxygen consumption of fish weighing 1 kg, we will arrive at a different conclusion. If the weight is 1 kg $= 10^3$ g, a carp will use $0.343 \times 10^{3 \times 0.85} = 0.343 \times 10^{2.55} = 0.343 \times 355 = 122$ ml O_2 per hour at 20°. But a salmonoid fish, by a similar calculation, will consume only 97 ml O_2, i.e. less than a carp of the same weight.

Therefore, in order to be able to compare the metabolic levels of different fishes it is not enough to have at one's disposal only metabolic rate measurements made at one particular weight. We must also know how the metabolism of each species is related to weight. In order to compare the metabolic levels of different fishes easily, the rates of respiration of fish weighing 1 g and 1 kg were computed by means of the appropriate equations and are presented in Table 17. These two weights cover the range that is most common in actual measurements of respiration.

Among the species considered in Table 17, at a weight of 1 g the highest metabolic rate is exhibited by salmonoid fishes (138% of the average for the table), then follow the sturgeons (109%) and, in third place the carp. Carp come first (138% of the mean) at a weight 1 kg, then follow the sturgeons and lastly the salmonoids.

[page 138] At first sight such a result seems strange, and contradictory to usual conceptions. However, it was obtained from a large amount of material, using a strictly objective method. I cannot see how to avoid a conclusion which flows from the actual data now available. It is possible that the relatively smaller decrease in the metabolic rate of carp with increase in weight, and hence the relatively greater metabolic rate of the large fish, is associated with the ability of carp to grow rapidly.

However, at this stage of our knowledge too much importance should not be attached to the differences which have been

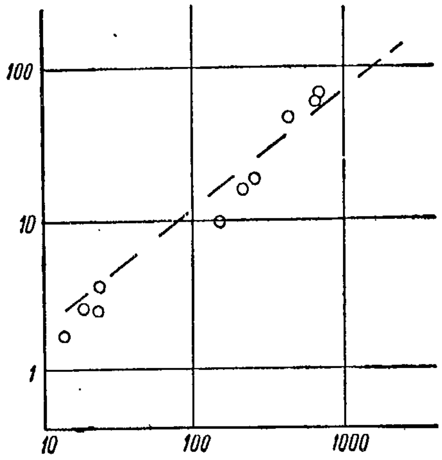

Fig. 43 [page 136]

Relation between total metabolism and body weight in elasmobranchs (Table 16). Axes as in Fig. 28.

The broken straight line indicates the average metabolic level for all fish (equation 7.3.5).

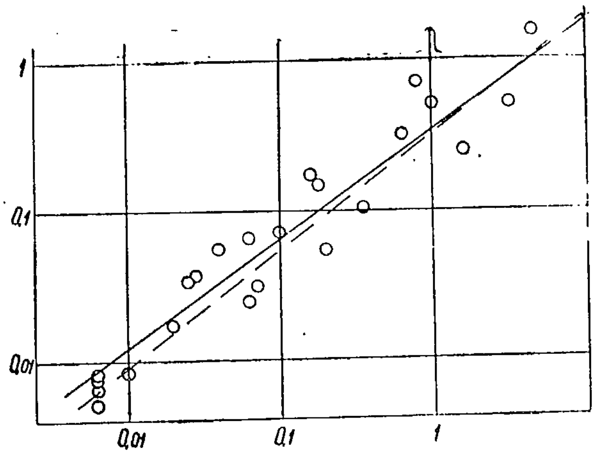

Fig. 44 [page 136]

Relation between total metabolism and body weight in young marine fishes, from the measurements of Zeuthen (1947). Axes as in Fig. 28.

The solid straight line is based on equation (6.2.3); the dotted line represents the average metabolic level for all fish (7.3.5).

observed. There is more involved than just the fact that observed differences among values of k and of a cannot always be regarded as reliable. In the statistical sense, k has been estimated for carp and sturgeons with considerable reliability. The differences between the values are real from this point of view. However we cannot limit ourselves to these formal considerations; rather we must try to consider, from physiological and biological points of view, the measurements which provide the initial material for all the computations.

A biological interpretation of measurements of fish metabolic rate is complicated by the fact that, with a few exceptions, the values obtained from an experiment represent not only the basal metabolism but to some extent also the movements and excitement of fish put into the respirometer. The relative importance of such additions to the basal metabolism can vary in different cases, depending on very many circumstances. To account for the experimental result shown in Table 17, it would suffice to postulate that circumstances were such that for carp the relative importance of movement [page 140] was greater for the larger fish, whereas in salmonoid and acipenserid fishes it was greater for the smaller fish. In that event, basal metabolism and the relation between metabolism and size might actually be the same in all three groups. I do not, of course, in any way insist on such an explanation, and bring up these considerations only to show that statistical processing of available data is not sufficient to demonstrate the reality of physiological laws. The true significance of the peculiarities of the material, and of the suggested relationships brought to light by these methods, must be further illuminated by special physiological investigations.

Regardless of how the problem of the differences in respiration between fish of different systematic positions will be resolved, the existing material is enough to support one conclusion right now: namely that, in general, the metabolic levels of fish of the most varied kinds are very similar. Indeed Table 18, which includes the extreme values of a for different fishes, shows that they do not differ from the mean by more than ±40%. In view of prevailing ideas about large differences in metabolism between different fishes, these limits must be regarded as unexpectedly small, especially if we remember that they may be partly caused by such a circumstance as a lesser excitability or mobility of some fish than others, during the experiments.

It is especially interesting that metabolic level is very similar in animals as remote in the scale of life as the various teleosts, the elasmobranchs (Fig. 42) and the cyclostomes (Fig. 35).

All that has been said about the similarity of the metabolic levels of different fish and fishlike creatures refers to data which mainly represent the resting metabolism. Therefore it would be altogether wrong to apply the conclusions above to the average metabolic level under natural conditions. For it can scarcely be doubted that the active metabolism, in contrast to the resting metabolism, exhibits characteristic and rather large differences between different fishes.

Chapter VII. [page 141]

The General Relationship between Metabolism and Body Weight of Fish

1. Comparisons within species and between species of the relation between metabolism and body weight of fish

The relationship of metabolism to body size, or weight, turns up when making comparisons both within species and between species. It is impossible to say in advance whether the relation of metabolism to weight in these two situations will be quantitatively alike, or different. For a solution of this problem we must turn to the actual data on hand.

It was shown by the material on respiration of carp (page 103) that within a species the degree of the dependence of metabolism on size, and hence also the value of the exponent of weight (k), can differ substantially depending on the conditions under which development takes place. Indeed, in particular cases, especially when the measurements cover a relatively small range of weights, the computations lead to different values of k within the same species. Thus, G. G. Winberg and L. E. Khartova (1953) found k = 0.98 for young carp; according to I. Kh. Maksudov's (1940) data, k = 0.63 for Gambusia; Bertalanffy (1951) accepts k = 0.67 for Lebistes; according to the measurements by Buytendijk (1910), k = 0.80 for respiration among sharks; from the data of T. I. Privolnev (1953, table 1), for young salmon k = 0.67. However, we repeat: in all these cases relatively small weight ranges are involved, and as a result many circumstances associated with the measurements can greatly affect the size of k.

The methodologically very meticulous work of Keys (1931) occupies a special position. The published results of 38 measurements of the rate of oxygen consumption of a small marine fish, Fundulus parvipinnis, show that in this case the metabolic rate decreased sharply as the weight increased. The reduction was so drastic that in spite of the small range of weights studied (1.2-11.2 g), it is easy to see that in this case k is equal to 0.4 approximately. It is interesting that the data of Wells (1935, fig. 16), which refer to the same species, also indicate [page 142] a change of metabolism with size that is much larger than usual. In this case, however, fish which lived in aquaria for two years are concerned; and toward the end of the experiment they died of disease. Keys obtained his material from a small body of water which was filled with water from the sea. It is possible that here too conditions for growth were unfavourable; hence it is still too early to be certain that such an unusually large change in metabolic rate with size is a characteristic of the species in question.

Only for carp can an intra-species comparison be made of respiration over a wide range of weights, and k proved to be 0.85±0.012. The data of V. S. and I. V. Ivlev (1952), which span two orders of magnitude, are also of interest. According to these authors, k = 0.81 for young salmon. We recall that for goldfish also k = 0.81, as computed from the data of many authors.

It is very important to bear in mind that the data on acipenserid and salmonid fish, discussed above, include the results of measurements of the metabolism of fingerlings and fry; furthermore the data for the fry and fingerling sevriuga (Table 5, Nos. 3-8, 25-30, 33-35) and osetr (Table 5, Nos. 1-2, 9-12), conform to the relationship common to all acipenserid fishes, namely k = 0.81.

Similarly the metabolism of fry and fingerling inconnu (Table 6, Nos. 17-20) and salmon (Table 6, Nos. 22-29) are rather well described by the general equation for salmonoid fishes, with k = 0.76.

Furthermore, although the material on the respiration of each of the more common species of freshwater fish (tench, roach, eel, perch, pike) are insufficient for computation of reliable values of k for each species separately, they nevertheless show very convincingly (Fig. 33-38) that the total metabolism of each of these species closely follows the general rule for all freshwater fishes, that metabolism increases in proportion to weight to the power 0.8.

The relationship between the total metabolism and the weight of a fish, obtained experimentally, can be interpreted in either of two ways. It could be postulated that a weight exponent close to or equal to 0.8 is typical of all fish, and indicates the general relation between metabolism and size. In that case the individual instances where metabolism changes more than this with size, or less, would be ascribed to secondary causes, or to the conditions under which measurements were made. The other interpretation is that in different subjects metabolism varies with size to different degrees, which is manifested experimentally in the different values obtained for k. At present it is impossible to say which of the two points of view is closer to the truth. We must be satisfied with the statement that, from the data available, in making comparisons within species the total metabolism [page 143] is in general proportional to the weight raised to a power close to 0.8.

In order to judge the nature of the relation of metabolism to size or body weight in comparisons between species, it would be necessary to compare the rate of metabolism of representatives of species differing in size but not in stage of development. For this the data presented in Table 18 for convenient inspection and comparison do not suffice, for they concern fish of different species and at different stages of development.

Nevertheless, in spite of the mixed material, it has seemed possible to establish the existence of a definite relationship---sometimes a very close one---between body weight and metabolism for each of the groups studied. Further, this quantitative relationship seems basically very similar to that encountered in the within-species comparisons studied above. This shows convincingly that the quantitative aspects of the relation between metabolism and weight is expressed in a similar way within species and between species. An analysis of separate series leads to the same conclusion. For example, the data on acipenserid fishes (Fig. 31), which are especially valuable because they were obtained for a very broad range of weights and show a close approximation of the points [to the line], to a considerable extent represent the respiration of *adult* fish of the various species (sterlet, osëtr, sevriuga and ship). The same applies also to the material on the respiration of salmonoid fishes (trout, salmon, smelt, whitefish, muksun, inconnu and others). In the same manner also the material for marine fishes (Fig. 40-41) could almost all be used to show the nature of the relation between metabolism and weight on an interspecific basis.

In all these cases the values of k found for individual groups differ somewhat from one another. However, the magnitude of the associated errors shows that the probability of any real difference is small even between the extreme values of k. There is still less reason to put faith in the deviations of individual values of k from the mean value for all fish obtained from the entire material. This very important circumstance shows clearly that one must not pay attention to small differences in the parameters of equations derived from empirical data.

In keeping with the material at hand, it can be taken as a first approximation that, in making comparisons between species, the total metabolism of adult fish of different sizes is proportional to their weight raised to a power of approximately 0.8. This is the same result as was obtained when we examined the relation of metabolism of fish of different sizes within a single species.

Therefore, in comparisons both within species and between species, total metabolism is usually [*page 144*] proportional to weight raised to the power 0.8, approximately, and the *rate* of metabolism is accordingly proportional to weight raised to power -0.2.

2. The metabolic rate of fish of different ages

From the fact, established above, that the relation of metabolic rate to body weight is much the same for comparisons within species and between species, there follow some important basic conclusions.

It is known that among higher vertebrates also the relation of metabolic rate to body size and weight is similar in the two cases. However, homoiothermy and early cessation of growth, and long life at a definitive size, constitute peculiar conditions which make a comparison with fish difficult.

Therefore it is our intention to use for comparisons data on poikilothermic aquatic animals. From a general biological point of view it is rather interesting that the material on the metabolic rate of Crustacea also indicates a great similarity or even identity of the metabolism-size relationship within and between species (Winberg, 1950). Zeuthen (1947) came to the same conclusion, on the basis of a large number of measurements of metabolic rates of various invertebrates and some data on the respiration of fishes.

This is an important conclusion. It means that the metabolic rate of a fish in the course of its individual development changes, in general, only to the degree which corresponds to its increase in size and weight. In other words, age [as such] has no influence on metabolic rate. Actually, after studying the available material on fish metabolic rate from this point of view, all of whose details cannot be mentioned here, we could not discover any data which either directly or indirectly indicated an effect of age on metabolism. Of course, it is not necessary to consider the many statements made by authors who have, quite without evidence, ascribed the changes in metabolism that accompany growth to the influence of age, or those who have simply been ignorant of the need to differentiate between the roles of these two factors (Streltsova, 1951; Gordienko, 1953). For example, in the Conclusions of O. L. Gordienko's work we read: "The oxygen consumption of fingerling beluga changes with age". This, of course, is true, but only in the sense that it is a statement of fact. For the size of the fish also changes with age. Hence if metabolic rate changes only to the extent that is required by its change in size, there is no [page 145] reason to speak of a relationship between metabolic rate and age.

It is evident that when studying the influence of age on metabolic rate we at the same time also touch upon the relation of the metabolic rate to stage of development [etap razvitiĩa], especially in considering the initial period of postembryonic development. In recent years much attention has been given in Soviet ichthyological literature to the stages [or stanzas] in the development of fish. The problem has been dealt with primarily by morphological methods. Nonetheless one often encounters the facile opinion, expressed in dogmatic form, that the various stages should also differ in respect to "rate" or "intensity" of metabolism ["skorost" ili "intensivnost" obmena], but without defining what exactly is meant by these terms. The attempts that have been made to identify physiological changes occurring when the organism passes from one stage to another mainly concern the later stages of embryonic development or the early periods of postembryonic life, i.e. stages of development which are not considered here. I. P. Shamardina (1954) showed conclusively that the metabolic rate rises during the fish's embryonic development and attains its maximum at the change-over to the postembryonic period, in which growth of the alevin is accompanied by a decrease in metabolic rate.

Similarly Yu. I. Cheprakova (1954) showed that the metabolic rate of goldfish fry attains its maximum at the time of the transition to active feeding and decreases rapidly afterwards. In trying to obtain confirmation of the opinion of V. V. Vasnetsov, that "the development of a fish does not take place gradually, but proceeds by leaps", Cheprakova maintains that within each of the stages of the early period of development the amount of oxygen consumed by a larva remains almost constant. However, she "failed to establish any clear relationship between the oxygen consumption per milligram of wet weight and stage of development".

V. I. Olifan (1945, 1945a) says that she has succeeded in discovering "critical periods" and a "periodicity of development" during the early stages of the postembryonic development of sevriuga and the Baikal omul. Unfortunately, on studying Olifan's material it is easily seen that no importance can be attached to it. For instance, in her table 2, which shows "respiratory changes in relation to age for fry of Baikal omul" the weight of the individuals is not indicated. After computing the weight of these we find, to our amazement, that when measuring the respiration of fry 12 days old, individuals weighing 8 mg were used, whereas on the next day the average weight of the fry used was 7.2 mg. A day later they weighed only 4.9 mg(!). At the age of 16 days the average weight was [page 146] 6.9; at 17 days, 6.6; and at 19 days, 6.4 mg. Then, unexpectedly, on the 22nd day we encounter fry which weighed 169 and 65 mg, and in the last experiment on the 32nd day the weight was 30.5 mg. Moreover her table 2 appears to contain typographical errors, for example in column 2, lines 4, 5 and 18 from the top. It is perfectly clear that with such material, not mentioning the other very doubtful aspects of Olifan's technique, it is impossible to decide how metabolic rate changes as the fry of Baikal omul develop. Similar remarks can also be made concerning Olifan's (1945a) material on the metabolic rate of young sevriuga. On different dates data for different series are cited, which differ in respect to [experimental] conditions; or averages from an unequal number of observations from different series are cited. This naturally leads to irregularity in the results of the measurements. From the data of her table 1, it is possible to compute the wet weight of the larvae and the corresponding rates of growth (C_v). The curve which shows the relation of C_v to age differs in respect to the position of its maxima and minima from the curve shown by Olifan in her figure 2, where the C_v values are computed on a dry weight basis. All this and other considerations make it impossible to regard the "periodicity" of development suggested by Olifan as convincing, the more so as the boundaries of stages IV and V given in the text do not at all agree with those depicted in her figure 1. Nor do the positions of the periods of increased oxygen consumption shown in figure 1 agree with the text on page 59.

Questions of great general biological importance and interest have been raised in Olifan's papers. It is quite possible that many of the statements she makes will be confirmed and extended by subsequent research. However, on the basis of the material at hand it is impossible to decide which of the described fluctuations and differences in metabolic rate and in growth indices really reflect true changes in metabolism when passing from one stage to another, and which are caused simply by fluctuations and differences in the experimental conditions, random deviations of individual measurements, and other secondary causes.

Only when material becomes available which admits of no doubts will it be possible to decide whether there are actual quantitative differences in metabolism at the different stages of development. Such material is still lacking, so in what follows we must consider the question in a more general form and try to establish whether the metabolic rate of fish is determined by the total size of the body or by their age.

An answer to this question can be obtained by measuring the metabolic rate of fish of the same age but different sizes, and of fish of different ages but the same size.

[page 147] In spite of the early stage of our knowledge of this question, it is possible to cite instances which show that fish of the same age but of different sizes actually have different metabolic rates. For example, in the work of T. I. Privolnev (1947, tables 10-13) we find the results of measurements of oxygen consumption rate of carp of the same age but belonging to different size groups. These measurements are included in our Table 4, Nos. 26-28. They agree perfectly with the results expected from formula (5.4.1).

No. (Table 4)	Weight of fish in g	Rate of metabolism	
		Expected	Actual
26	39	0.198	0.198
27	12.5	0.234	0.254
28	2.5	0.298	0.280

In the Conclusions of his 1953 paper, dealing with the young of Baltic salmon, the same author writes: "The physiological indices change greatly in relation to size among fingerlings of the same age."

It would be easy to select a number of examples from Tables 3-16 to show that respiration of small species of fish (verkhovka, Fundulus, and others) does not differ from the respiration of fingerlings of larger species of fish of similar size, but much younger in age. The results of our measurements of the oxygen consumption rate of young carp are presented in Fig. 30. Among these data there are also points for determinations of the rate of oxygen consumption by young and adult verkhovka (Leucaspius delineatus) carried out at the same time. Figure 30 shows that the adult verkhovka have the same metabolic rate as young carp of the same weight.

On the whole, the conclusion that age does not have any detectable influence upon the rate of oxygen consumption by fish seems to be supported by the aggregate of all available data. Of course this does not necessarily mean that no age differences in metabolism will be found in future. The data at hand mainly concern fish that are at rest or are swimming slowly. It is not impossible that age differences in metabolism will come to light in the course of studies of the quantitative aspects of the metabolism of actively moving fish.

If fish of one age but different sizes do in fact differ to the same extent in metabolic rate as do fish of the same sizes but different in age, [page 148] we must conclude that the differences in rate of growth have no noticeable effect upon metabolic level. Such a conclusion contradicts the hypothesis that when growth is slow--as a result of insufficient food for example--the metabolic level should be lower than that of more rapidly growing fish of the same size and weight, but younger in age; as was observed by us during the aquarium experiment with young carp.

It is possible that the retarded rates of growth of fishes which mature early, such as Fundulus or the viviparous fish [such as Gambusia or guppies] (page 123), is associated with their exceptionally rapid decrease in metabolic rate with size. However, as has been pointed out, it is not certain that the data at hand are typical of the growth of these species under conditions that are normal for them. Furthermore, our data for verkhovka (Fig. 30), taken under natural conditions, did not show any rapid decrease in metabolic rate with size.

At the moment it is hard to understand how the present contradiction will be resolved: between the data that compel one to admit that age practically does not affect metabolic rate, and the common idea--which is supported by some facts--that when growth is retarded metabolic rate is lower. It is possible that, within "normal" limits of variation in growth rate, the metabolic rate depends mainly on size, but under conditions that greatly inhibit growth the metabolic level too is lowered. Only by carefully conducted investigations will it be possible to fully delineate the relationships among metabolic level, growth rate, age, and size, which are closely related to one another during the normal development of a fish.

Regardless of how this problem will be resolved in the future, it is clear that, in studying it, it is necessary above all to take into consideration the normal relationship of metabolism to size and weight of the fish.

3. The "basic equation" relating metabolism and the body weight of fish

The similarity of the relationship between metabolism and weight, as compared within species and between species, and the relatively insignificant differences between the metabolic levels of different fishes, makes it possible, after combining all the material, to get an equation that describes the relation of mean metabolic rate to body weight for all freshwater and marine fishes. For all of the 369 pairs of values (Tables 3-16) we get:

$$k = 0.78 \pm 0.0096; \qquad \text{and } Q = 0.316w^{0.78} \qquad (7.3.1)$$

[page 149] However, there are important reasons to suppose that the value $k = 0.81$, found for freshwater fish, is closer to the true mean for all fish than is the one obtained from all the data (0.78). It must be taken into consideration that the values included in the tables for freshwater fish are for the most part averages of many measurements. Therefore, much more weight should be attached to them than to the material on the metabolism of marine fish which consists mainly of individual measurements. Furthermore, the data by Zeuthen on the metabolism of the young of marine fish, which consist exclusively of single measurements of the rate of oxygen consumption of very tiny fish, have exerted great influence upon the magnitude of the value k calculated for all fish. Perhaps it would be more correct to average these data [and use them as a single point], in which event their relative weight would be 25 times less and thus they would not have so large an effect on the result of the calculation. Excluding Zeuthen's data, we get from all the remaining 364 values for marine water and freshwater fish:

$$k = 0.815 \pm 0.0105; \qquad \text{and } Q = 0.285w^{0.81} \qquad (7.3.2)$$

Since Zeuthen's data occupy an extreme position they greatly affect the result of the computation. This example shows how little importance should be attached to small differences in k and a. Moreover, in this instance the difference is not even statistically significant, since the difference between the values of k (0.03) is less than 3 times its mean square error (0.014). Therefore there is every reason to assume that the relation between the mean value of total metabolism and weight, for all fish, can be expressed as a first approximation by the following simple equation:

$$Q = 0.3w^{0.8} \qquad (7.3.3)$$

Besides Ivlev's work mentioned above (page 127), which pertains to freshwater fishes, the literature contains another attempt to construct a curve to describe the relationship between metabolic rate and weight by generalizing some of the available data (Zeuthen, 1947). Zeuthen's curve is based on his own measurements of the respiration of young fish (page 134) and a few data from the literature. Zeuthen makes use of data obtained at different temperatures (11-20°) without any adjustment. Among others, he also used the entirely unrepresentative and erroneous data of Terroine and Delpech (page 89).

The metabolic rates of fish of various weights read from Zeuthen's curve, and those computed by equation (7.3.3), are compared below:

[page 150]

Weight of fish in grams	0.01	0.1	1	10	100	1000
Metabolic rate, from Zeuthen	0.97	0.51	0.24	0.11	0.075	0.050
Metabolic rate, from equation (7.3.3)	0.75	0.47	0.30	0.19	0.120	0.075

In its right-hand part Zeuthen's curve comprises data which for the most part were obtained at temperatures considerably lower than 20°. Bearing this in mind, as well as the fact that his curve was drawn by hand using few points, agreement between the readings on his curve and our data must be regarded as unexpectedly good. This is an additional argument in favour of the fact that equation (7.3.3) sufficiently accurately represents the relationship, common to all fish, between mean metabolic level and body weight.

Thus until more accurate data become available we have every reason to accept this equation as a basis for making provisional calculations of expected values of fish metabolism at any given weight. If:

$$Q = 0.3w^{0.8}$$

we obtain thence for the metabolic rate:

$$\frac{Q}{w} = 0.3w^{-0.2} \qquad (7.3.4)$$

or in logarithmic form:

$$\log Q = 0.8 \log w - 0.523 \qquad (7.3.5)$$

$$\log\left(\frac{Q}{w}\right) = -0.2 \log w -0.523 \qquad (7.3.6)$$

In future we shall use this expression repeatedly in computing the expected values of metabolism for a given body weight. Therefore it is reasonable to call equation (7.3.3) the "basic equation", purely for convenience, of course. For the same reason we will call the values of metabolic rate obtained from the basic equation the "routine metabolism", because we wish to emphasize that it is a matter of the average results of measurements of metabolism by diverse methods, which differ from the true values of the resting metabolism to a degree that probably differs for different experimental materials.

For general orientation it is convenient to note that, according to the basic equation, when weight increases 10 times the metabolic rate is reduced by 21%. In order to reduce the metabolic rate 10 times the weight must increase 100,000 times, for example, from 10 mg to 1 kg.

[page 151] The interrelations discovered between metabolism and weight, represented in the form of parabolic equations, indicate only the relation of the mean values of metabolism to the weight of the fish, and do not exclude the possibility of considerable deviations in metabolic rate among individual experimental subjects. The results of each separate measurement will deviate more or less from the expected mean. The principal value of the relationships discovered is that we have, for the first time, a fully objective criterion for evaluation of the level of respiration of different subjects. It now becomes possible to decide whether any experimentally found value should be regarded as a high, or a low, rate of metabolism. Appraisal of the influence of various factors on metabolism is also made easier. Further, it becomes possible to characterize quantitatively the specific peculiarities of the metabolism of different species or different stages of development.

Let us now see what the likelihood is of the deviation of an individual observation from the expected mean. In order to answer this question we shall calculate the mean square error (Σy) of the straight [line]:

$$\log Q = 0.78(\log w) - 0.500$$

obtained from equation (7.3.1):

$$\Sigma y = \sigma_y \sqrt{1 - r^2} = 1.008 \sqrt{1-0.974^2} = 0.228$$

As is well known, one can estimate that at a high level of probability (0.997), all the individual values of y (log Q) deviate from the value estimated from the equation by not more than $\pm 3\Sigma y = 0.684$. Transforming the scale from log Q to Q, we find that individual values of Q can differ from the anticipated value by not more than 4.83 times in either direction. This determines only the extreme limits of maximum deviations, which can occur only very rarely. For the normal distribution 50% of all the deviations do not go beyond the limits of $\pm 0.675\Sigma y = \pm 0.154$. Transforming from log Q to Q, we find that in 50% of the cases the individual values for total metabolism of fish will differ from the value found by the equation by no more than 1.43 times in either direction, i.e. they will deviate within the range of +43% to -28% from the value obtained from the basic equation. We see that the relationship discovered between total metabolism and the weight of the fish, when properly understood, does not exclude the possibility of considerable deviations in individual cases, that may result from peculiarities of the species or other causes.

Similar computations for the equations applying to individual species or groups of fish show that in cases where the scatter of the points is small and the correlation coefficient is large the values found by experiment should lie much closer to the expected mean. For example, for acipenserid fishes:

$$\Sigma y = 1.426\sqrt{1-0.997^2} = 0.110$$

[page 152] In this case 50% of the results of measurements will differ from the expected values of Q by not more than 1.2 times, i.e. they will lie within the range of +20% to -17% deviation from the computed value. Even the extreme limits of the deviations of the results of measurements ($\pm 3\Sigma y = 0.33$) can differ--in this case--from the computed value by only 2 times in both directions.

Σy for the other series are given in Table 18. Using them, it is easy to obtain from appropriate statistical tables the probability of any deviation from the computed value in each case.

However, all that has been said will be applicable to new measurements only if new data follow the same distribution as those from which the relations described were deduced. If methods of measurement or other conditions are changed, then the distribution of the new data could be altogether different. In particular, it is clear that the dispersion of the values used reflects, to a considerable extent, inaccuracies and possibly even errors made by various authors in making their measurements. Hence there is no doubt that material which represented only real differences in metabolism characteristic of different species would lie much closer to the average values. In other words, the possible differences in the intensity of metabolism of different species should show very much less deviation from the mean values than is suggested by the mean square errors of the equations mentioned above.

The results of statistical processing of experimental data must be used with discretion. Statistical methods are absolutely necessary when one has to deal with a large number of values that show considerable dispersion. However, when statistical methods are used without fully understanding their possibilities and the limits of their rational application, they invariably lead to a purely formal description of the external aspect of a phenomenon.

If it is continually borne in mind that all the expressions obtained above, and equation (7.3.3) in particular, provide only an approximation to the expected mean values for fish metabolism, as far as they can be determined on the basis of material available, they can be used successfully to study the quantitative aspects of that metabolism. It becomes possible to eliminate the influence of differences in size upon metabolism when comparing the metabolic rates of different materials, and to appraise values obtained in an experiment by comparing them with an expected mean value.

In order to facilitate such tentative computations, and also to show more clearly the degree of dependence of metabolism on weight, I have prepared Table 19, [page 153] in which are gathered together values for total metabolism (Q) and also metabolic rate $\left(\frac{Q}{W}\right)$, computed from the basic equation (7.3.3).

By using the basic equation, or Table 19, along with Table 1, it is easy to get the expected values for the total metabolism and the metabolic rate of a fish of any weight at any temperature from 5° to 30°. I must emphasize again that values estimated in this way are useful because they help to evaluate and to compare experimental data, and not because they can replace the latter.

However, in some cases, for example when solving problems concerning the calculation of a water supply for, or the aeration of tanks containing, live market fish or young fish, it is enough to know approximate mean values for rate of oxygen consumption. Such approximate values can be obtained with much greater confidence from the basic equation or from Table 19 than from the results of a few, frequently very casual, measurements--such as are often used for these purposes in practice.

4. A comparative evaluation of the level of metabolism of fishes

Now that the level of metabolism characteristic of fish can be regarded as established to a first approximation, it becomes possible to compare fish metabolic rates with those of other representatives of the animal [page 154] kingdom, on the basis of generalized average data rather than from individual values that are frequently unreliable. We will limit ourselves to a comparison with crustaceans and with warm-blooded vertebrates.

On the basis of comprehensive data--his own and those in the literature--G. G. Winberg (1950) found that for crustaceans:

$$Q = 0.105w^{0.81} \text{ at } 15°; \qquad \text{or } Q = 0.165w^{0.81} \text{ at } 20°$$

However, in the same work it is pointed out that measurements of metabolic rate made with freshly-caught material lead to somewhat higher values. In these cases $a = 0.15$ at 15°, which corresponds to 0.236 ml O_2 per gram per hour at 20°.

Since the exponent in the relation of metabolism to weight is practically the same in fish and crustaceans, we can estimate the ratio of the mean metabolic levels of these two groups from the ratio of the proportionality coefficients (a). For fish, a = 0.316; for crustaceans, a = 0.165, or perhaps more accurately, 0.236. Observe the relatively small difference in the metabolic levels of fish and crustaceans; that for fish being somewhat the higher. However, as has been emphasized repeatedly, we do not know by how much the values for routine metabolism exceed the actual value of the basal metabolism. It will be recalled that in the results, given above, of 3 special determinations of basal metabolism, two of them carried out with goldfish and one with a salmonoid fish (pp. 99-107), it was found that basal metabolism comprised about 60% of the routine metabolism obtained from equation (7.3.3). If, for lack of other data, 60% of 0.316 is taken, we will find that on the average a = 0.25 for the basal metabolism of fish. This value puts the metabolic rate of fish and crustaceans still more nearly on the same level. We have cited this somewhat artificial example mainly to indicate a direction for further research on this problem. For the time being it is better to stick to the statement that, judging from available measurements, in view of their almost equal exponents in the relation between metabolism and size, the average level of metabolism of fish is 35-90% higher than the average for crustaceans.

From a large amount of material amassed by many authors, it has been shown that the relation of the basal metabolism of various warm-blooded vertebrates to body weight is well expressed by the equation:

$$M = 70w^{0.74}$$

where: M is the total metabolism in Calories per day, and w is body weight in kilograms.

[page 155] For an animal with a body weight of 1 kg, M = 70 Cal/day. This corresponds to a consumption of 583 ml O_2 per hour.

According to the basic equation the routine metabolism of a fish weighing 1 kg is equivalent to an oxygen consumption of 75.3 ml per hour at 20°. Consequently when comparing the basal metabolism of a mammal weighing 1 kg with the routine metabolism of a fish of the same weight, it will be seen that the metabolic rate of the fish is 7.74 times lower.

The question arises whether this difference can be ascribed entirely to the difference in the temperature (20° and 37°) at which metabolism takes place in the two cases. We cannot supply a completely unequivocal answer to this question; however, there is this consideration. In order for metabolism to differ by 7.74 times, with a difference in temperature of 17°, it is necessary that the Q_{10} should average 3.3 over the interval concerned. The value of Q_{10} would be larger still if it were possible to make a comparison of the basal metabolism of warm-blooded animals not with the "routine" metabolism of the fish, but with their "basal" metabolism. In most cases values of Q_{10} at high temperatures are considerably smaller [than the above], usually around 2. Hence we may conclude that the high metabolic rate of warm-blooded animals cannot be explained solely by their high body temperature. It would seem that, along with their ability to maintain a body temperature close to 37°, the high level of metabolism of warm-blooded animals is brought about also by other means.

The questions raised regarding the level of metabolism characteristic of representatives of large taxonomic categories are of primary importance from a general biological point of view. It is evident that the answers will influence basic ideas regarding the nature of the changes in metabolism during evolution, and about common physiological traits that are peculiar to the representatives of various large subdivisions of the animal kingdom.

A discussion of these questions far exceeds the scope of this book. They should have separate treatment, in the same way as the question of what factors determine the relation of metabolism to size must be studied separately. For either problem, the solution will require, firstly, drawing upon data characterizing the quantitative aspect of metabolism not only of fish, but also of other divisions of the animal kingdom, and, secondly, including in the discussion not only the data concerning resting metabolism or values close to it, but also material concerning active metabolism. We regard the latter as very important. Without serious consideration of the energetics of actively moving animals, and the accumulation of sufficient authentic quantitative data of this sort, it will be practically impossible to explain how metabolic rate has changed during the course of evolution or to understand fully the significance, nature and causes of the relation of metabolism to body size in animals.

[page 156] I might add that it will not be easy, for the purposes outlined above, to make use of the extensive material on metabolic rate of various kinds of poikilothermic animals available at present, primarily because of their utter lack of orderly arrangement.

The generalization of data at hand, the search for the best methods of expressing the quantitative aspect of metabolism, and decisions on what problems should be given priority in research in the various large subdivisions of the animal kingdom, are the next important tasks for comparative physiology. As I see it, by helping to reach these objectives for fish, I have assisted in clarifying some quantitative principles of great importance to general biology; these have now been brought out into the open, even though they are still imperfectly understood.

Chapter VIII. [page 157]

The Level of Metabolism of Fish of Different Ecological Groups

1. Ecologically-determined differences in the metabolism of fish

Before considering ecologically-determined differences in fish metabolism it is necessary to say something about the difficulties encountered along the way, which have often led to insufficiently proved and even inaccurate conclusions. The following considerations are of importance.

In the first place, very often when processing and evaluating data, not enough consideration is given to the well-known fact that great fluctuations occur in measurements of metabolic rate even in duplicate experiments, carried out under what seem to be identical conditions.

Secondly, often not enough attention is paid to the importance of the weight of the animals used in the experiments, in spite of the fact that the general nature of the influence of body size on metabolic rate is well known.

Thirdly, it is not always kept in mind that differences in metabolic rate may be a result of a greater liveliness and excitability of some fish, as compared with others. Therefore the results of measurements carried out by the usual methods can be very close to the resting metabolism for some fish, with some slight bias toward active metabolism, while for others they can greatly exceed the resting metabolism. Such differences might easily be ascribed to different ecological conditions.

In the fourth place and finally (and this is most important, even when all the experimental conditions and methods of handling the material have been observed, which are necessary in studies of a quantitative nature) prevailing methods for the study of fish metabolism make it possible to know only the metabolism of relatively motionless fish--whereas ecological differences should primarily be concerned with active metabolism. From this the conclusion follows that, since active metabolism of fish has as yet been barely touched on by research, the elucidation of ecologically [page 158] determined differences in metabolism remains almost entirely a task for the future.

Nevertheless this question is often discussed, and frequently the opinion is voiced, in special articles and textbooks of a general nature, that there are large ecologically-caused differences in metabolism between fishes. Many authors, if not all, apply this even to resting metabolism. Therefore it is advisable to discuss this question using a few specific examples. This will at least make it possible to appreciate the basis for the frequent assertions about the great differences in metabolism between different fishes.

Lack of attention to the importance of body size, which invariably affects metabolic rate, greatly reduces the value of the data of many works. For example, D. N. Taliev (1947), in some cleverly designed investigations, gives the results of measurements of metabolic rate of a number of species of Baikal sculpins at low temperatures. These data would have been of much greater value had the author also mentioned the weight of the experimental fish. However, the weight of the fish is not stated, and all the author's conclusions based upon a comparison of the metabolic rates of different fish remain completely unconvincing because it is not clear whether the differences he found may not be associated simply with differences in size of the fish of different species, rather than with their habitat and mode of life, as the author believes. This undervaluation of the importance of size (weight) of fish does not always appear in as extreme a form as that of authors who discuss differences in metabolic rate but fail to state the weight of the fish used in their experiments (Taliev, 1947; Tauson, 1949; Markova, 1949). Sometimes the weight of the fish used in the experiments is stated, but is not used in the evaluation of the data, for example in the work of M. T. Ivanova (1939); who, in addition, gave no consideration to the possibility of random variation in the results of her measurements, and ascribed all the differences between her various experiments on metabolic rate to the effects of different modes of life and local environmental conditions. Ivanova believes that fish living in stagnant water have a lower metabolic rate than river fish. However, though this view is true to a certain extent, it does not follow from her material. The only conclusion that might be reached after a careful analysis of her data is that, judging by only one or two measurements, the respiration rates of crucian carp, tench, loach and spiny loach were lower than those of the other species studied. If the different weights of the fish used in the experiments are taken into consideration then, contrary to Ivanova's belief, it is impossible to discover any consistent differences in the metabolic rate on the basis of her data.

T. I. Privolnev (1951), in his pamphlet on the biotechnics of shipping live fish, furnishes a table of the "respiration rates of fishes", which also contains information [page 159] on the amount of water required for the normal respiration of these fish, computed from the metabolic rates. The table contains data for 13 species and gives weights for only 3 of them. It is interesting that for the ide two values are given: the first for "ide more than 4 years old" and the second for "ide weighing 100-135 g". The pike are divided into two groups: "large pike" and "small pike". For the other 7 species mentioned it is not clear to what weight or size the data in the table refer. For this reason it is impossible to judge whether the figures for metabolism contained in the table reflect species characteristics or merely differences in the size at which fish of the various species are commonly transported. For lack of indication of the weight of the fish, it is impossible to compare these data with other material. However, if the eel be excluded--for which species the lowest value is quoted--the differences among all the other figures are small--from 50 to 135 mg O_2/kg/hour at 10°. This, according to the same table, corresponds almost to the difference between the metabolic rates of fingerling carp of 22-35 g and yearling carp of 320-325 g. For the former, the rate of oxygen consumption at 10° is 120 mg O_2/kg/hour, and for the latter it is 65 mg. We may notice in passing that if we compute the mean metabolic rate for carp of these sizes by equation (5.4.1), reduce it to 10° and express it in mg O_2/kg, we obtain the figure 111 for a weight of 28.5 g and 77 for a weight of 320 g. These are very close to the values cited in Privolnev's table.

I take this opportunity to remark that, inasmuch as species differences in metabolism are overshadowed by the differences in metabolism of different size groups, any figure which expresses the metabolic rate of fish must always be accompanied by an indication of the weight of the fish, and of course the temperature, to which it refers.

Unfortunately these absolutely essential conditions are often ignored in textbooks and articles of a general nature. For example, G. Kh. Shaposhnikova (1950) asserts that "trout at 10° consume 100 cm^3 of oxygen per day per kg of weight, and at 15° they consume 220 cm^3" (Zhizn' Presnykh Vod SSSR, vol. 3, page 731). These values are completely absurd. From what has been said above it can easily be seen that even the largest trout have a metabolic rate many times larger. Unfortunately, such examples are not isolated cases.

In order to understand how those often completely erroneous views concerning the metabolic rate of different fish become established, that are given in fisheries literature, we cite the following example. It is stated in many textbooks that the metabolic rate of trout is considerably greater than that of carp, resting metabolism being meant. The view that trout have an especially high resting metabolism is not in the least supported by the factual material on the metabolism of salmonoid fishes, including [page 160] trout, collected in Table 6 and in Fig. 32. Lindstedt's (1914) measurements are the source of the wrong impression concerning trout metabolism. The work of Lindstedt, one of the first detailed works on fish metabolism, was published in a very widely read German fishery magazine, and so became very generally known. Lindstedt's data, unlike much other material on fish metabolism, have found their way into all the summaries, and are constantly quoted. This author obtained high values for the respiration of rainbow trout, so he wrote that the rate of respiration in trout is higher than in other fishes. However, let us see under what conditions his measurements were made. Lindstedt used the circulating gas method. In a roomy respirometer of 52.7 litres' capacity the fish could move about actively during the entire experiment. In describing his material, Lindstedt remarks that one of the trout continually chased the others, with the result that a large fraction of the fish died before the end of the experiment. On page 219 we read: "During the first experiment this 'malicious' trout . . . . injured a smaller fish so badly that it died on the second day after the experiment. During the second experiment the largest fish raged so furiously that on the second day after the experiment it became too weak to be used for a representative experiment." The author himself draws attention to the exceptionally high data of one of the experiments and believes that they are due to the fact that "during the experiment a large trout chased after the other fish with unceasing zeal". It is no wonder that under such conditions a high oxygen consumption rate was obtained. In all, three successive measurements were made using the same material. All four fish were involved in the first measurement, three in the second, and in the third the two surviving fish. Since Lindstedt's data have been included in summary tables, they have been cited along with other values, without any indication of the conditions under which they had been obtained, and have been accepted in the same way as corresponding data for tench, carp and other slower and less excitable fish which would have a metabolism close to their resting metabolism even in Lindstedt's apparatus. With regard to pike, Lindstedt makes a point of mentioning that they remained "ideally quiet" in the respirometer.

Though this is an extreme, almost anecdotal, example, nevertheless in many other cases too the differences between data compared and used as a basis for conclusions could have had a similar origin. For up to the present no adequate attention has been given to the need to differentiate strictly between resting metabolism and active metabolism, to the possibility of random fluctuations in the results of measurements, and to the effect of the different weights of the subjects used in experiments.

For this reason it is not necessary to attach importance to many statements, by various authors, if they are expressed [page 161] in such a form as, for example: "It has been established by our experiments that the respiration rate of young osëtr is considerably lower than that of sevriuga" (Olifan, 1940). Possibly this is true. However, although she is considering the quantitative aspect of metabolism, Olifan presents no quantitative data. Hence it is not clear what is really meant, to what degree the difference is expressed, or how the reality of the observed difference was established, and so on.

There is still another difficulty not mentioned above, which cannot be eliminated even if all the conditions listed are observed. Under the influence of individual acclimation to conditions of the environment the level of metabolism can change, as happens in the event of acclimation to temperature (page 40) or to the oxygen content in the environment (page 64). As a result, differences in metabolism between two subjects that result from their being kept in different environments prior to the experiment, can easily be misinterpreted as a manifestation of a species difference.

The recently published results of a small-scale investigation by G. L. Shkorbatov, L. P. Azanovich and G. V. Losovskaia͡ (1954) are particularly pertinent in this connection. These authors, seizing a convenient opportunity to obtain under natural conditions young of wild carp and pond carp, some of both types of which had been reared in running water and still water respectively, measured the oxygen consumption rate of these fish, and obtained measurements within the following ranges for each group of fish used in the experiment (mg O_2/g/hour at 20°):

	Fish that had lived	
	in still water	in running water
Wild carp	0.135 - 0.189	0.217 - 0.316*
Pond carp	0.154 - 0.182*	0.259 - 0.274

The weight of the fish of each of the 4 groups used in the experiment varied within the same limits (4-16 g), so that in this respect the results of the measurements are fully comparable. In this case there is an exceptionally clear demonstration of the relation of level of metabolism to the conditions under which the fish had developed, whereas there is no difference in the metabolic level between wild carp and pond carp which had grown up under the same conditions. Under the different conditions the metabolism changed either to the same degree, or very similarly, in the two forms. However, the authors rightly point out that lakes and rivers are the normal environment for wild carp, and ponds for pond carp. Therefore wild carp and pond carp taken from their normal habitats (marked by * in the schedule above) differed with respect to the level of metabolism. This could easily be ascribed to constitutionally fixed peculiarities of the metabolism of these forms.

[page 162] It is interesting that the figures obtained by Shkorbatov et al. correspond perfectly to the routine metabolism expected for fish of that weight. According to the fundamental equation the routine metabolic rate should be close to 0.20. This is somewhat greater than the values obtained for fish from quiet water and less than the metabolism of fish from flowing water.

A subsequent work of Shkorbatov's (1954a) contains interesting data on the metabolic rate of young whitefish raised in a carp pond where the surface temperature of the water rose to 29°, and also in a reservoir where the water "remained at a temperature not greater than 17°". The fingerlings raised in the pond, weighing 11-12 g, had a metabolic rate which when measured at 20° was equal to 0.203 ml O_2/g/hour. This is slightly above the routine metabolism expected from the fundamental equation (0.18). Carp fingerlings raised in the same pond (weighing 8-14 g) had a metabolic rate 26% lower than that of the whitefish (0.151 ml O_2/g/hour at 20°). The whitefish fingerlings raised in the reservoir, of about the same weight, had a metabolic rate of 0.273 ml O_2/g/hour at 20°, i.e. higher by 34% than that of the fingerlings that had developed in the pond. It seems that in this case the difference was caused by the different temperatures in the pond and in the reservoir, as well as by differences in oxygen, and various other conditions.

A different result was obtained by the same author for the sterlet. Part of the fish were kept for two months at 8-10° with an oxygen content of 10-12 mg/l, and the rest at 15-18° and 4-8 mg/l. The corresponding oxygen consumptions were 0.231 and 0.212 ml O_2/g/hour at 17° (the number of measurements and the weights of the fish were not indicated). In this case the conditions of temperature and oxygen under which the fish were raised had an unexpectedly slight effect upon the metabolic rate.

A lowering of the metabolic rate in the case of fish raised in ponds was also described by T. I. Privolnev for young Baltic salmon. In this case, for fish of the same weight (5 g), the oxygen consumption rate of fish raised in ponds was 75% of that of those taken from the Salatsa River.

In stating that metabolism is lower for fish in quiet water, we still have no reason to ascribe this to the direct action of the current upon metabolism, since conditions in quiet and running waters differ in many ways. This circumstance is often underestimated. For instance, it is not uncommon to read in reviews and textbooks that Washbourn demonstrated an effect of current on the metabolic rate of fish. Actually this author measured the rate of oxygen consumption of narcotized trout fingerlings, of which one group had been reared for 80 days in a tank with swiftly circulating water, while the other group was kept in a tank with slowly circulating water. In the second case somewhat [page 163] smaller values were obtained (respectively, 0.116±4.5 and 0.91±7 ml O_2/g/hour at 10°). The average weights of the fish of the two groups (6.7 and 5.8 g) indicate that in the "slow-circulation" tank growth was slower. It is likely that oxygen conditions also differed. Therefore it is quite possible that it is this factor, and not the direct influence of rate of the flow of the water, that caused the differences in the respiration of these fish (Washbourn, 1936).

V. B. Adrianov (1937), in discussing the results of his measurements of the oxygen consumption rate of perch, roach, crucian carp and carp, also believes that his data indicate a lower metabolic rate in fish which inhabit quiet water. However, if this work is carefully perused it becomes clear that the data obtained are altogether inadequate to support this conclusion--even though it may be true. The respiration of the roach and perch was measured on the second day after the fish had been caught; that of crucian carp was measured after they had been kept in an aquarium for 15-20 days; and that of carp was measured in winter after they had been kept under artificial conditions for a long time. Furthermore, the weight of the perch and roach was 15-20 g, while that of the carp was 113 g. It is evident that under such conditions it is impossible to explain the observed differences in metabolic rate simply by differences in ecology of the fish used in the experiments. These cases deserve attention because examples of inadequately proven conclusions regarding the metabolic rate of fish are frequent, especially when physiological data are quoted in the course of descriptions of the biological peculiarities of different economically-important species. Such conclusions, repeated endlessly in summaries and textbooks, soon begin to be regarded as well-established principles.

Differences in metabolism can be regarded as well established only if they are obtained from a sufficiently large number of measurements carried out under identical conditions, and either on animals of the same size or with the effect of size taken into consideration. This latter, however, can only be done now that the relation of metabolism to size has received a quantitative formulation. And even in cases where differences in metabolism have been established by objective methods, it must be stated to what extent they depend upon the conditions under which the material used in the experiments was reared.

2. The metabolic rate of fish that differ ecologically

The question of the influence of ecological conditions on fish metabolism has two aspects. Firstly, it can concern changes in the metabolic level resulting from individual acclimation [page 164] to various conditions of the environment. Secondly, it can be a matter of species adaptation, i.e. constitutionally fixed differences in metabolism which reflect the different environmental conditions to which different species of fish have become adapted. The influence of individual acclimation to various environmental factors on metabolism was discussed earlier (pp. 40, 157, etc.). There mention was also made of the possible results of species adaptation to temperature, which according to some data involves a lowered level of metabolism in tropical fishes. We must now enquire to what extent species adaptation to different environmental conditions is developed in respect to metabolic level among fishes.

The largest ecological differences among aquatic animals are associated with life in salt water as compared with fresh water. It is natural that repeated attempts have been made to compare the metabolic rates of marine and freshwater animals, and marine and freshwater fishes in particular. Different authors have expressed different opinions concerning this matter, all of them equally ill-founded. The present trend is to believe that freshwater animals have the higher metabolic rate. Contrary opinions have also been expressed (Bounhiol, 1905).

On the basis of our material we will now try to find out whether there is sufficient reason to believe that the metabolic level of marine and freshwater fishes differs. Equations which express the mean metabolic level of marine (p. 136) and freshwater (p. 127) fishes have been cited above. We may recall that from the entire material we obtained:

$$\text{for marine fish, } Q = 0.321\, W^{0.79}$$

$$\text{for freshwater fish, } Q = 0.297\, W^{0.81}$$

It is hardly necessary to prove once again that there is not the slightest reason to ascribe any significance to the small differences between the parameters of these two equations, which summarize the results of much work done by many authors, working independently at different times and in different countries.

The question of the relative metabolic rates of marine and freshwater fishes, which has excited a vast amount of discussion, can be regarded as solved. The average level of metabolism is the same in marine and freshwater fish.

It is interesting that the same conclusion was finally reached regarding the metabolism of freshwater and marine crustaceans (Winberg, 1950).

The identity of the average level of metabolism in marine and freshwater fishes does not at all exclude the possibility that there exist, within each of these two groups, even quite large ecologically-determined differences in level of metabolism in different species.

[page 165] Because of inadequate data we are not able to make any statement about the metabolic level of species of marine fish that differ ecologically. The material on the metabolism of freshwater fish contains more along this line. The boundaries of the possible differences between the routine metabolism of species adapted to different environmental conditions have to a considerable degree already been presented above, in discussing the material on a taxonomic basis. The average routine metabolism of groups having a different ecological profile, such as the salmonid and cyprinid fishes, was very similar. It is probably even more significant that when there are sufficient data to estimate the average level of routine metabolism of individual species, no great differences have been discovered. The metabolic levels of such diverse species--in the ecological sense--as carp, perch, pike, crucian carp, and others (Fig. 7-12) are very similar, to say the least.

Consequently, the values for routine metabolism, if they do differ as between fish of different ecological groups, do so to only a slight degree. In connection with this, bearing in mind all that was said above (page 157) about the need to observe a number of conditions strictly when comparing levels of metabolism, it is not easy to find convincing examples that demonstrate ecologically-determined differences in metabolism of different species of fish. For this purpose it is possible to compare only the data obtained by one author, from fully comparable material. In the work of A. G. Mints (1952) we find the results of the measurements of the oxygen consumption rate of fingerlings of crucian carp, carp, perch and dace of about the same weight (9-11 g). The average of 5 experiments provides us with the following values for the metabolism of these species: 0.17, 0.25, 0.23 and 0.36 mg O_2/g/hour at 16.5°. Judging by these figures the metabolism of the crucian carp fingerlings is half that of the dace, while carp and perch occupy an intermediate position. We may observe that Mints' data couldn't agree better with the figures for routine metabolism expected from the basic equation--because the latter coincide with the values for fingerling carp and perch, which according to the experiments occupy an intermediate position.

Authors who have used the flowing water method have some interesting statements regarding ecologically-determined differences in metabolism. Clausen (1936) found that if the 8 species of fish he examined are arranged in order of decreasing metabolic rate, a series is obtained which coincides almost perfectly with the order in which they appear in the river from the headwaters down to the mouth. This means that the fish inhabiting swiftly flowing waters have the higher metabolic rate. In this case differences in metabolism, obtained from a considerable number of separate measurements, are quite strongly developed (the extreme values are in the ratio of 1:3). They cannot be associated with the relatively slight differences [page 166] in the weight of the experimental fish (for Clausen's average data see Table 8, No. 33-35, 49, 50; and Table 11, No. 14-16). It might seem that these data can be regarded as an acceptable indication that there are ecologically-determined differences in routine metabolism of fish. However doubts arise, firstly, because of the wide range of the differences discovered by Clausen, and secondly, because of the very low values he quotes, the highest of which only just approximate to those expected from the basic equation for fish of that weight. We must wait for confirmation of these data, which were obtained from species of fish whose respiration, as far as I know, has never been studied by anyone else.

It must be remembered that a low metabolic rate is characteristic of tench, according to the data of several authors (page 113). It appears that the same applies to crucian carp (Table 8, Fig. 34). Perhaps it can be regarded as established, or at least very likely, that typical limnophilic fish have a routine metabolic rate lower than average, whereas typical rheophiles have a higher one. However, it is hard to say how widely this rule can be applied, how large a circle of species it embraces, or to what extent the level of metabolism differs in extreme and typical cases; and furthermore, what are the relative roles of individual acclimation and species adaptation. It seems to me that the level of metabolism of rheophilic fish could scarcely be more than 1.5-2 times that of limnophilic fish.

In general it must be admitted that there are as yet very few reliable data from which it is possible to estimate differences in the level of metabolism of fish of different ecological groups.

From the fact that levels of routine metabolism of species which differ ecologically are often similar or even identical, we should by no means conclude that under natural conditions there are no ecologically-determined differences in the metabolism of different fish. On the contrary we have every reason to believe that they can be strongly developed, but not in respect to resting metabolism, which mainly determines the magnitude of the routine metabolism--instead, in respect to active metabolism. Ecological differences concern first and foremost the moving, active fish; they determine his mode of life and degree of activity. To a much larger extent than can the resting metabolism, the active metabolism reflects the multiformity and specificity of different kinds of adaptation--to prolonged or brief periods of movement, to movement at a constant or at a changing speed, at different efficiencies, and so on. The study of ecologically-determined differences in metabolic rate will be put on a sound foundation only after systematic research on active metabolism has been pursued.

Chapter IX. [page 167]

The Level of Active Metabolism of Fish

1. Introduction

Little is known about the active metabolism of fishes. Research into it has encountered many difficulties so that, in the main, the task still lies in the future. Methodological difficulties can be overcome if the necessary attention is given to this problem. For this reason a study of active metabolism of fish should be regarded right now as a top-priority objective in the ecological physiology of fish. We might even say that there is no need for additional accumulation of data on the metabolic rate of fish under conditions of weak activity or nearly resting, because not one of the basic problems of theoretical or practical interest, for which fish respiration is measured, can be solved in that manner.

The study of the metabolism of fish is of practical interest in that it is one of the possible ways of determining the food ration. Furthermore, quantitative data on fish metabolism are needed to solve a number of questions concerning fish behaviour, the biotechnics of raising fish in ponds and reservoirs, wintering fish [in ponds], shipping live fish, etc. In all these situations one must have information, not on the resting metabolism, but values which reflect the metabolism of fish at that degree of activity that is characteristic for the prevailing conditions. All this is well known. Less attention has been given to the fact that not one problem in the ecology and physiology of fish that is associated directly or indirectly with metabolic rate can be solved successfully without knowledge of the active metabolism. For example, the significance of temperature under natural conditions, and also when fish are being raised artificially, is primarily determined by the influence of temperature upon the active metabolism, which is regulated by different laws than the relation of resting metabolism to temperature (page 171). It was shown in Chapter IV that it is impossible to understand the relation of respiration to partial oxygen pressure, if the difference between the resting and [page 168] the active level of metabolism is not taken into consideration (page 56). It is especially important that the problem of the limiting oxygen concentration in water, which because of its practical significance has given rise to a large, but highly contradictory, body of literature, cannot be moved out of its impasse until the degree of the activity of the fish and the level of active metabolism are taken into consideration in determining the critical oxygen content.

In exactly the same way any attempts to establish a relationship between the level of metabolism and such morpho-physiological peculiarities of fish as, for example, the quantity and quality of their hemoglobin, hematological indicators, the structure and functional properties of the respiratory apparatus, etc., cannot be successful if they are based only upon knowledge of values of the resting or the routine metabolism.

In these cases, as well as when studying ecologically caused differences in fish metabolism, we come across manifestations of species adaptations which were developed by the fish while in an active state, and which therefore only indirectly and to a much less degree can, in some cases, also affect the level of the resting metabolism. In this connection some observations of Gray (1947, 1954) are extremely apropos, which show that the relative area of the gills parallels the degree of the activity of the fish. In an active fish, Brevoortia tyrannus, the gill area per gram of weight is 10 times greater than that of a slow-moving fish (Opsanus tau), and when computed per square centimeter of body surface it is 15 times greater. It is evident that this is primarily associated not with the difference of the resting metabolisms of the two species, but rather with their different levels of maximum active metabolism.

Finally, the actual magnitude of the resting metabolism can only be established with certainty if it is possible to know the metabolism at different degrees of activity, and from these to discover the minimum value that corresponds to least activity.

All these considerations convince us that data describing the metabolism of actively-moving fish are of great interest.

2. The metabolic rate of actively swimming fish

Let us now review what is known at present regarding the quantitative aspect of the active metabolism of fish. There is no need to stress the opinion of many authors that an active fish has a higher level of metabolism, or to confirm this well-known fact by illustrations. Such illustrations, which could easily be furnished, would not supply the answer to the fundamental question, namely, how much does metabolic level [page 169] rise in relation to degree of activity? An answer to this question can be expected only from special investigations.

The work of V. P. Pentegov, Yu. N. Mentov and E. F. Kurnaev (1928) is of exceptional interest in relation to the energy expenditures of keta or chum salmon during their spawning migration, when ascending the Amur River. A special expedition along the whole length of the spawning migration of the keta up the Amur River (1200 km) took samples of the fish and subjected them to a detailed chemical analysis. Further, the speed at which the fish moved and the speed of the current of the river were also established in certain sectors. Energy expenditures were calculated on the basis of weight loss and the results of chemical analyses. For the whole distance, on the average, they amounted to 28390 cal per kg of weight per day for females, and 25810 cal for males. The average weight of all the fish collected at the various stages of migration was 5033 g for males and 3955 g for females.

Water temperatures of the Amur River are also given in this work. During the entire period of sampling the temperature of the water was close to 12°. Let us accept the mean data for salmonoid fishes as the basal metabolism for keta. Then from equation (6.1.2), after a transformation to 12° using Table 1, we find that for males of the abovementioned weight the metabolic rate is 0.0283 ml O_2 per gram per hour and for females it is 0.0297. The abovementioned values of energy loss can be easily translated into the form to which we are accustomed; for males it is 0.215 ml O_2/g/hour, and for females it is 0.236. Therefore, the ratio of the active metabolism during migration to the routine metabolism found from formula (6.1.2), is 7.6 for males and 7.9 for females. The true value of the resting metabolism is likely somewhat less than the routine metabolism computed from the average data for salmonoid fishes. Therefore, the true ratios must be correspondingly higher.

Thus in this case the active metabolism of fish weighing 4-5 kg, when moving for a long time at an average speed of 114.6 km per day, or 1.33 meters per second, exceeds the routine metabolism by 7-8 times at least. It is of interest that Lindroth (1942), on the basis of his experience in studying the metabolism of fish, believes that during active movement the metabolism of fish is increased 7 times. However, he does not support this with any data.

Substantial material on the active metabolism of fish is contained in the works of some North American authors, mostly Canadians (Spoor, 1946; Fry, 1947; Fry and Hart, 1948; Graham, 1949; Gibson and Fry, 1954).

Spoor, who studied the changes in the activity of fish over 24 hours by means of a special device (page 79), also considered rate of oxygen consumption in his most recent series of experiments, along with automatic recording [page 170] of the fish's activity. The fish were kept for a considerable length of time (weeks) in a well-isolated chamber which had circulating water. In order to avoid excitement, which affects the activity of the fish, the pipes that carried off the water from the chamber were long (10 feet), and together with the wires from the device that registered the disturbance of the water [caused by the fish] they led into an adjoining room. These conditions made it possible to establish what metabolic rate corresponds to periods of different degrees of activity. A large part of the measurements depicted in Fig. 45 refer to a goldfish which weighed 32 g. Spoor drew by eye the straight line which indicates the general trend of all the 59 points.

[page 171] The intersection of the line with the ordinate axis makes it possible to determine the basal metabolism. This quantity corresponds to practically complete lack of motion of the fish, when the sensitive recording device did not disclose any turbulence in the water. This quantity is regarded by Spoor, with some justification, as the true value of the resting metabolism (page 96). He suggests that his method be adopted for determining the resting metabolism of fish. This author pays less attention to the values that were obtained when the fish was very active. It can be seen from Fig. 45 that during maximum activity the metabolic rate was about 4.5 times the resting rate.

Fry and his co-workers in the Ontario Fisheries Research Laboratory (Canada), where many valuable experiments concerning the ecological physiology of fish have been carried out, developed in their experimental work a definite system of relationships, which were presented in a general article in 1947. Here and in a subsequent publication (Fry and Hart, 1948) we find a very interesting consideration of the relation between metabolism and activity in fish. From extensive experience in studying the acclimation of fish to different temperatures, and research on fish respiration done [page 172] at the above Laboratory, Fry considers it necessary, when studying the effect of different factors in metabolism, not to be limited to "standard" or resting metabolism, but also to study metabolism at the maximum level of activity. Furthermore, he points out that in all such studies it is necessary to reckon with the prior experience of the organism, i.e. to consider the effects of acclimation on the action of each of the factors considered. He is of the opinion that in order to study the position of the optimum of any activity[1] of the organism, considered as a physiological property of the species, it is first of all necessary to acclimate the organism to each level of the factor that is examined. As an illustration we show (Fig. 46) the shift in optimum temperature for maximum speed of movement of goldfish, in relation to temperature of acclimation.

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[1] Fry uses the English word "activity" in a sense that can be most closely translated by the common term "function" [funktsiia].

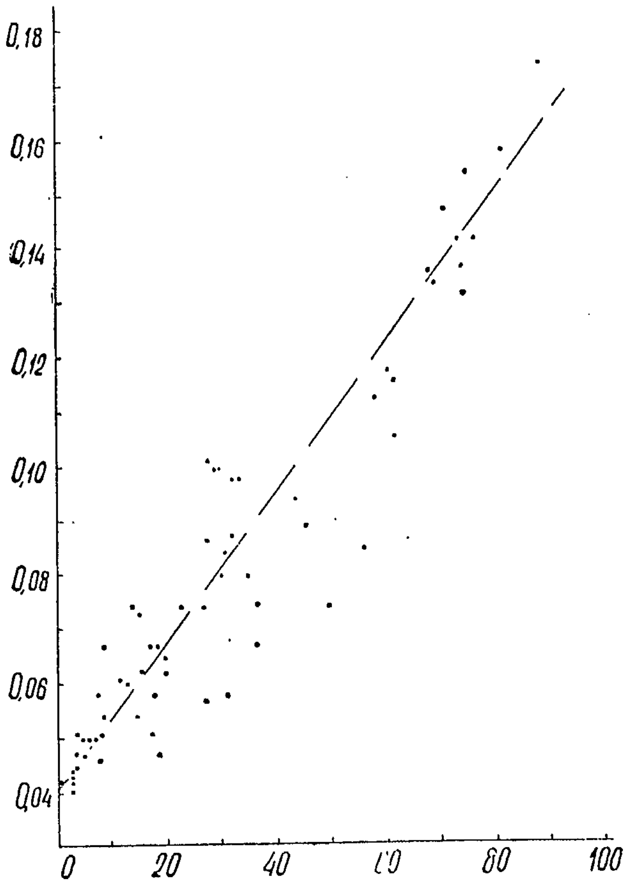

Fig. 45 [page 170]

Relation between the metabolic rate of a goldfish and its degree of activity.

Abscissa--number of marks made by the recording device per minute; ordinate--oxygen consumption in ml/min at 23-25°. The weight of the fish used in the experiment was 32 g (Spoor, 1946).

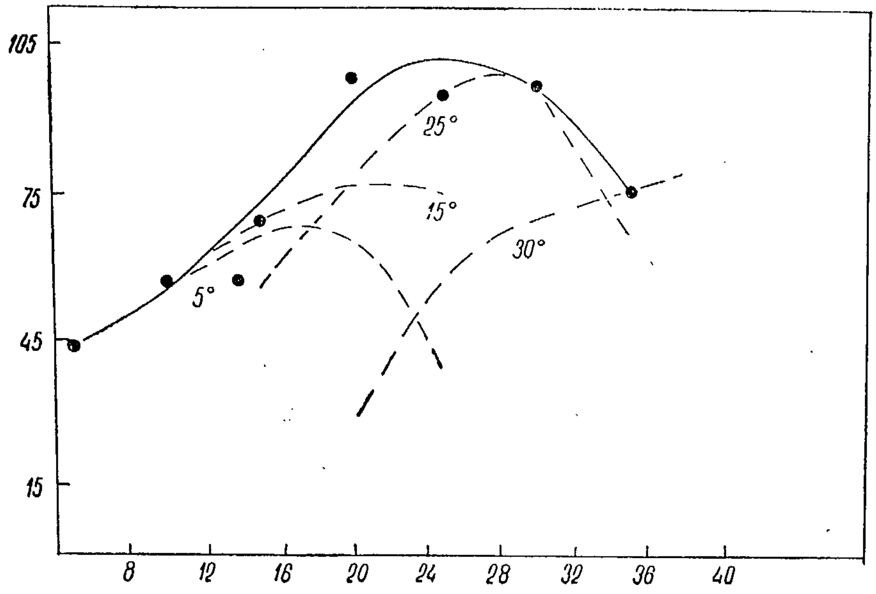

Fig. 46 [page 171]

Relation between the maximum possible metabolism and temperature, among swimming goldfish acclimated to different temperatures.

The upper solid curve refers to fish that were acclimated beforehand to each experimental temperature (Fry, 1947).

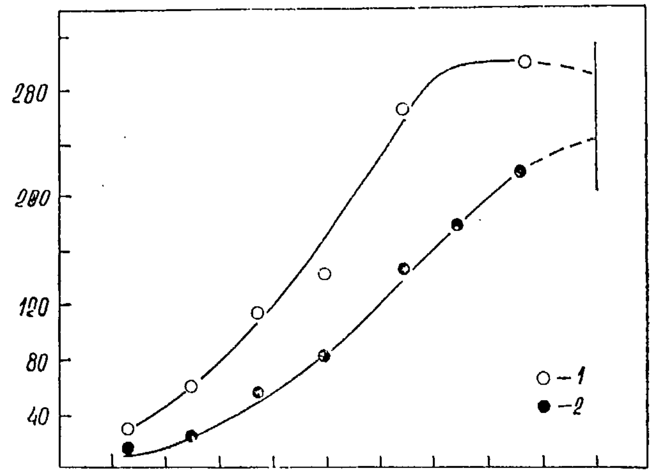

Fig. 47 [page 172]

Relation of resting metabolism and active metabolism to temperature, in goldfish.

Abscissa--temperature; ordinate--the rate of consumption of O_2 in ml/kg/hour. 1- active metabolism; 2- resting metabolism (Fry and Hart, 1948).

The speed with which the fish moved was studied by means of a special device whose principal component was an annular vessel rotating on bearings, with outside walls of glass [actually, transparent plastic]. The fish, swimming against the current and orienting themselves with respect to a source of light, were compelled to swim at a speed that could be regulated easily by the speed of rotation of the vessel. The same device [page 173] was also employed for the simultaneous measurement of active metabolism (Fry and Hart, 1948). In that event the vessel was covered with a circular lid. The lowest level of metabolism in the diurnal cycle was accepted as the resting metabolism. The latter was obtained by hourly measurements in the closed vessel, equipped with pipes to supply and drain off the water.

By this method the very interesting data shown in Fig. 47 were obtained from goldfish acclimated beforehand to each of the temperatures examined. It is noteworthy that at high temperatures the active metabolism is related to temperature in a different manner from resting metabolism. The very great general importance of this fact for understanding the effect of temperature under natural conditions is obvious. At high temperatures the two curves approach each other. However, this does not happen in the case of all species; for example, the similar data for the bullhead (Ameiurus nebulosus) do not exhibit [page 174] any such approach of the two curves close to lethal temperatures (Fig. 48). It is especially interesting that the difference between the active and the resting metabolism of the goldfish is also reflected in the curve showing the relation of maximal speed of motion to temperature (Fig. 49). On this basis, which must be regarded as sufficiently substantial, Fry concludes that not the active metabolism in itself, but only the difference between the active and the resting metabolism, comprises the energy basis for movement. From this point of view the optimum temperature for movement is situated in the zone where the difference between the active and the standard levels of metabolism reaches a maximum. Finally, at a certain high temperature, the rates of active and of resting metabolism come together. This means that it is impossible to provide any greater metabolic rate than the high level attained when the fish are at rest, i.e. active movements are impossible. These interrelations are shown in Fig. 50 in a slightly diagrammatic form. In addition, on the same graph is shown the effect of still another factor, reduced ambient oxygen, as based on experimental data. The course of the curves shows that lowering the partial pressure of oxygen to 25 mm Hg is not enough to affect the resting metabolism even at high temperatures. However this is enough to lower the level of the active metabolism and, obviously, to cause a corresponding reduction of the speed of motion at high temperatures.

Finally, Fry (1947) draws attention to the fact that one must distinguish between power [moshchnost], which in our case is the difference between active and resting metabolism, and performance [otdacha] or utilized power, which in our case is the rate of movement. There is no necessary linear relationship or direct proportionality between them. [page 176] In fact, on the basis of the data in Fig. 46, 47 and 49, it can be said that the swimming speed of goldfish is not proportional to the difference between the active and resting levels of metabolism; instead, it [the maximum swimming speed] increases more slowly--in proportion to the square root of this difference (Fig. 51).

Fry's data show that at maximum speed of movement of goldfish whose average weight was 3.8 g, the active metabolism was not more than twice the resting metabolism. A much greater difference was indicated in the experiments of Spoor. It is possible that this is related to the fact that Spoor used much larger goldfish. It should be remembered [page 177] that, according to a number of authors, the relative energy expenditures for movement by aquatic animals grow smaller with decrease in size (Ludwig, 1928; Zeuthen, 1947). However, in the present instance this could scarcely be the only reason, or even the main reason. It might also be significant that Spoor's experiments involved short periods of great [page 178] activity, whereas Fry's involved continuous motion at constant speed.

Another species, the cold-water oxygen-loving American char, Salvelinus fontinalis, was investigated similarly using the same methods (Graham, 1949). Fingerlings were used of 17-65 g weight, average 27 g. As in the previous example, the fish had been fully acclimated to each temperature. The difference between active metabolism and resting metabolism exhibited even greater variation with temperature [page 179] (Fig. 52). Here also the degree to which the active metabolism exceeds the resting metabolism at different temperatures corresponds nicely with the change in maximum speed of movement at those temperatures (Fig. 53). In this work much attention is allotted to the relation between the maximum possible speed of movement and the degree of saturation of the water with oxygen at different temperatures. In this oxygen-loving species the active metabolism at high temperatures has already decreased at 75% saturation (Fig. 54). At 50% saturation the decrease in active metabolism is very pronounced at all temperatures, and at 20-25° not only is no activity possible, but death sets in as a result of asphyxiation. Below 75% saturation the maximum possible speed of movement of Salvelinus is reduced at all temperatures. This was not observed in the less oxyphilic goldfish, even at 25% saturation.

Figure 52 shows that the active metabolism of Salvelinus in the zone of optimal temperatures is more than 4 times

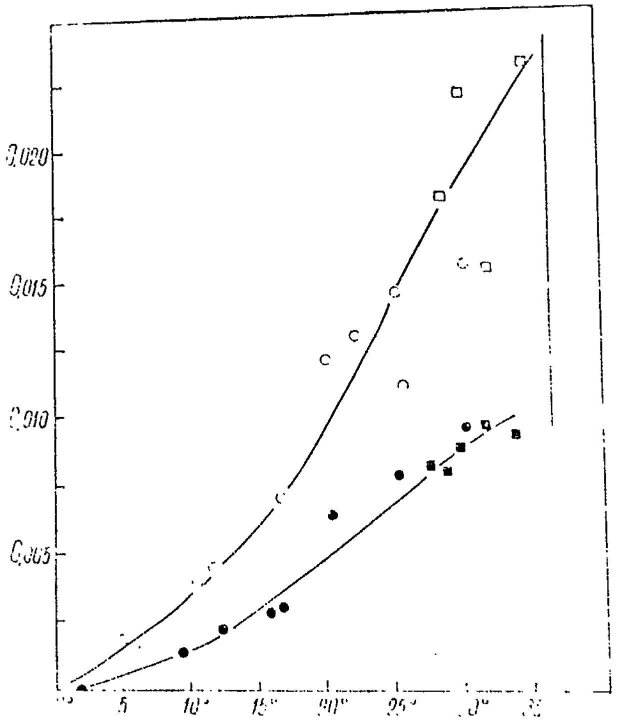

Fig. 48 [page 173]

Relation of the active metabolism (upper curve) and resting metabolism to temperature, in the bullhead (Ameiurus nebulosus).

Abscissa--temperature; ordinate--rate of oxygen consumption (Fry, 1947).

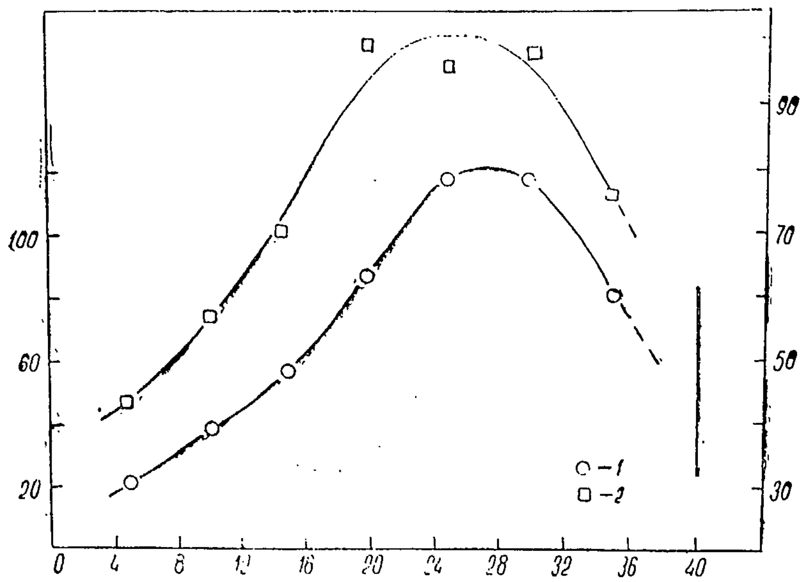

Fig. 49 [page 174]

Relation between maximum possible speed of continuous motion and temperature (1), and the difference between the active and resting metabolism (2), in goldfish.

Abscissa--temperature; ordinate--on the left, the consumption of O_2 in ml/kg/hour, and on the right, swimming speed in feet per minute (Fry, 1947).

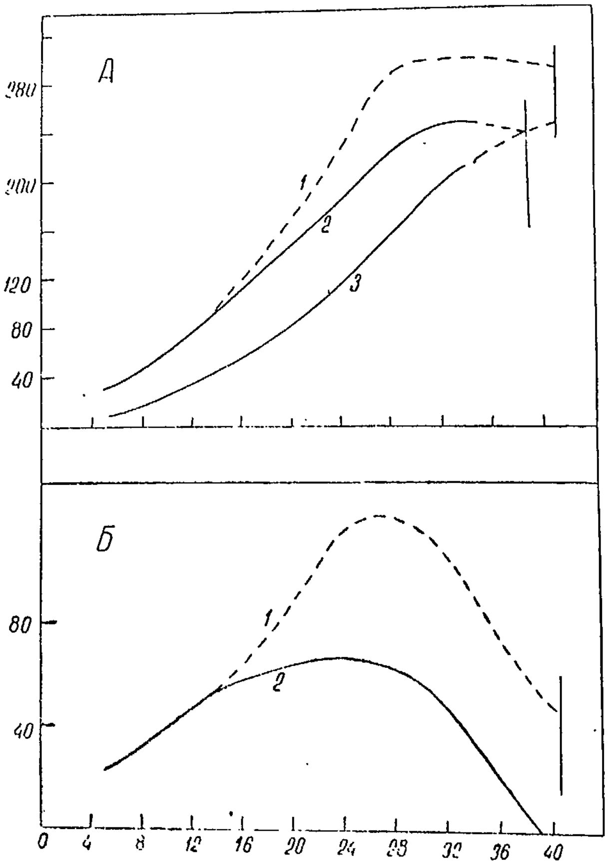

Fig. 50 [page 175]

A. Relation between the maximum possible rate of active metabolism and temperature at various ambient oxygen contents. 1--at a pO_2 of 40 mm Hg; 2--at a pO_2 of 25 mm Hg.

Б. Difference between the active and resting levels of metabolism under the same conditions.

Abscissa--temperature; ordinate--oxygen consumption in ml/kg/hour (Fry, 1947).

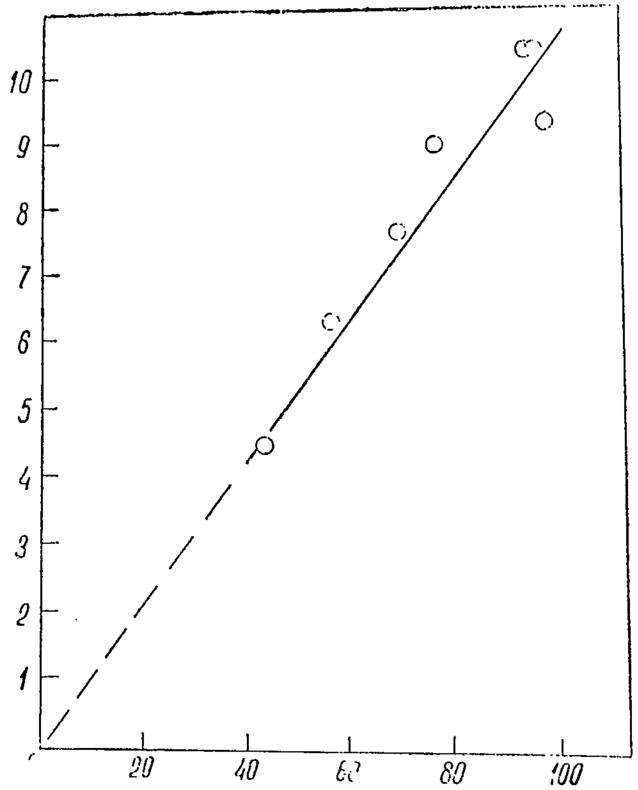

Fig. 51 [page 176]

The relationship between "power" (the difference between the maximum active metabolism and the resting metabolism) and "performance" (rate of movement) in goldfish.

Abscissa--speed of motion in feet per minute; ordinate--the square root of the difference between the two metabolic rates (Fry, 1947).

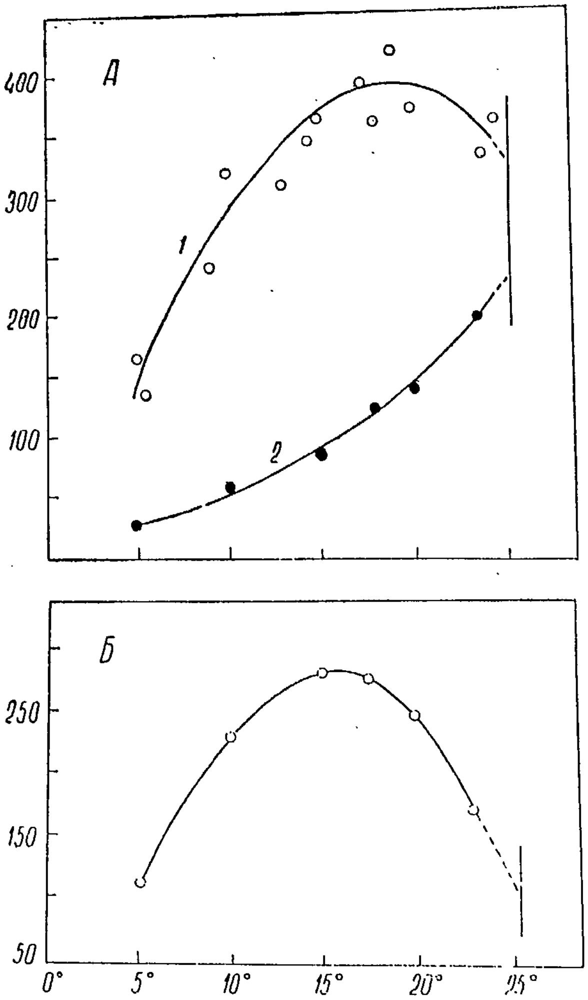

Fig. 52 [page 177]

Maximum intensity of the active metabolism (1) and of resting metabolism (2) of the American *Salvelinus fontinalis* at various temperatures (A), and the difference between them (Б).

Abscissa--temperature; ordinate--rate of oxygen consumption in ml/kg/hour (Graham, 1949).

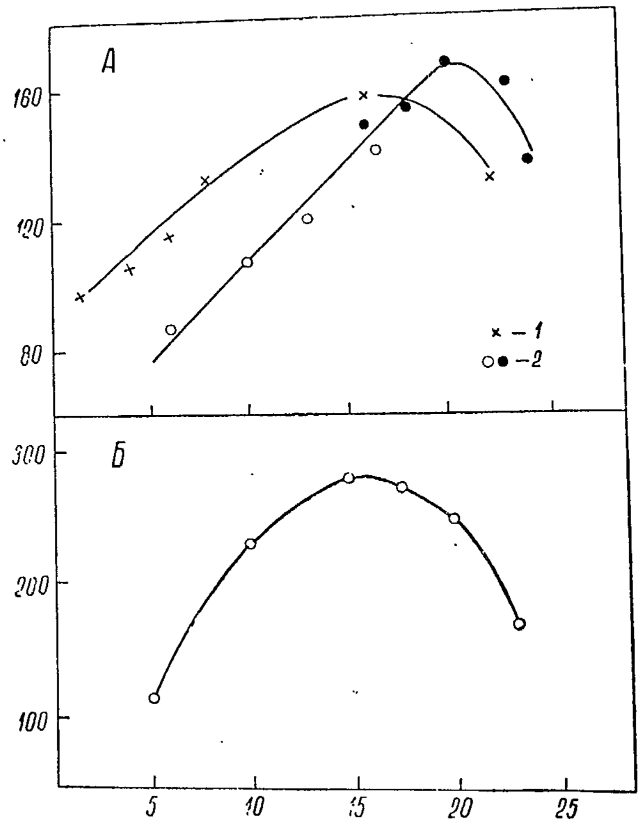

Fig. 53 [page 178]

The maximum possible speed of motion of Salvelinus fontinalis at various temperatures (A), and the difference between the active and the resting metabolism (Б).

Abscissa--temperature; ordinate--A: rate of movement in feet per minute; Б: consumption of O_2 in ml/kg/hour. 1- from Rogers' data; 2- from the measurements of Graham (1949).

higher than the resting metabolism. We should bear in mind that this applies to fish larger than the goldfish used in Fry's experiments, and to a faster speed of movement (about 160 ft/min, not 100 as in Fry's experiments).

3. Energy expenditures of fish in motion

[page 180]

We shall try to make use of the data given above to get at least a preliminary idea of the size of the figures which describe the expenditure of energy by various fish when they are moving.

For chum salmon we obtain appropriate values directly from the data above by reducing them by 1/8. By this method we come very close to the difference between the active and the resting metabolism. For Salvelinus fontinalis and goldfish we can derive this difference, and the speed at which fish move at optimal temperatures, from Fig. 49, 52 and 53. Thus we obtain the values presented in the last two columns of Table 20.

The computations shown in Table 20 are of interest as the first examples of empirical figures that make it possible to estimate energy expenditures of fish at maximum speed. It is hardly possible to discuss the significance of the differences between the various values. Perhaps it is more practical to observe that the energy expenditures per unit weight and per kilometer of movement were generally about the same for fish of different sizes. Bearing in mind that the calorific equivalent of 1 g of live weight of fish, in round figures, is close to 1000 cal, we may illustrate the result in a graphic manner by stating that at the expense of reducing their weight by 1%, fish of different sizes can swim 20 to 40 km under optimal conditions. Considering that the fat stores are the first to be expended, the actual loss in weight by fish that move but do not feed will be somewhat less.

All the data considered so far, bearing on the active metabolism of fish, were obtained without using any theoretical [page 181] concepts regarding the nature of the relationship between metabolism and movement. An altogether different approach to this question is found in the works of V. V. Shuleĭkin and his students. Shuleĭkin develops a theory of fish movement on the basis of which it is possible to estimate the energy used by a fish of a certain size when moving at a certain speed (the useful work), and also to estimate the maximum speed which, according to Shuleĭkin's concepts, can be attained by fish of different sizes.

L. A. Kovalevskai͡a (1952) made an attempt to apply Shuleĭkin's theory to experimental data. The metabolic rate of fish moving at various speeds was measured by means of a device of special construction. The fish were placed in a ring-shaped respiration chamber. The water in the chamber was set in circulation by a screw propeller. Kovalevskai͡a computed the "total expenditure of energy" from measurements of oxygen consumption of fish that were forced to swim against the current. The ratio of the "useful energy" computed on the basis of Shuleĭkin's theory, to the "total energy" found experimentally, Kovalevskai͡a calls the coefficient of useful activity [koeffitsient poleznovo deĭstva].

The horse mackerel (Trachurus trachurus) was used in the experiments. Measurements were made with fish of different sizes (length from 9 to 22 cm, weight from 7.5 to 72 g). The speed of the current varied from 0 to 1.2 m/sec. It is a matter for regret that Kovalevskai͡a carried out the measurements of respiration and interpreted them without taking advantage of the experience of earlier investigators, and without regard for the usual conditions for physiological experiments. Freshly caught fish were placed in a respirometer without the necessary period of acclimation to the conditions of the test. Furthermore, the test was very short, lasting only 10-15 minutes. Therefore, it is no wonder that for the resting metabolism, i.e. when the current speed was 0, data were obtained that are not in any way representative, for the extremes differed as much as 22-fold! Quite formal also are her equations of the type $O_2 = kv^n$, relating metabolic rate per gram of body weight (O_2) with the speed at which the fish move (v). It is obvious that with such a relationship, when $v = 0$, $O_2 = 0$, i.e. the resting metabolism is zero. Furthermore, even the values of k which Kovalevskai͡a obtained from her own data, for fish of different sizes, do not make sense biologically. According to these values, when $v = 1$ the fish should consume the following numbers of millilitres of O_2 per hour per gram of weight: at a length of 9-10 cm: 10^{-5}; at 13-15 cm: 6.6×10^{-4}; and at 17-18 cm: 1.4×10^{-3}. In the first place, these values are ridiculously small; and in the second place, it is impossible to imagine that metabolic rate should increase sharply with increase in size. Furthermore, a careful analysis of Kovalevskai͡a's experimental data shows that there is no reason to accept [page 182] her statement that they can be described satisfactorily by a parabolic equation; this is especially clear if the obviously erroneous data for $v = 0$ are disregarded.

Kovalevskai͡a also quite wrongly accepts as a measure of full power [polnai͡a moshchnost] not the difference between the active and the resting metabolism, as should be done, but the total metabolism. The inevitable result of this method of calculation is an increase in the "coefficient of useful activity" with increase in speed [of motion], at least for small rates of movement. A "coefficient of useful activity" calculated in this way actually has no meaning whatever.

These considerations make it impossible to accept any of Kovalevskaîâ's conclusions. It is as difficult to say how real are the results of her measurements of the oxygen consumption rate of fish at different rates of movement, the more so as there is not even any mention of the temperatures to which the data apply. In two instances very high values were obtained for fish of small weight (7.5 and 10.5 g), and in two instances very low values were obtained for large fish (51 and 72g). Seven other experiments with fish of various weights (from 14 to 64 g) produced very consistent values for the metabolic rate, which increase approximately in proportion to the speed of movement. Judging by these data the relation between oxygen consumption and speed can be expressed, very closely, as follows:

Speed, m/sec	0.5	0.75	1.0
O_2 consumption, g/hour	1.0	1.35	1.7

We should scarcely go wrong if we conclude that the rate of resting metabolism in this case, on the average, lies in the range of 0.15-0.3 ml O_2/g/hour. In that event the active metabolism will be 2.3-5.6 times the resting metabolism when the speed is 0.5 m/sec; and if the speed is 1.0 m/sec, it is 4.7-10 times. It would require 0.194-0.215 cal per gram of body weight to travel a distance of 1 km at a speed of 1 m/sec, which is close to the data of other authors (Table 20).

Regardless of the fact that Kovalevskaîâ's attempt at experimental confirmation of Shuleĭkin's theories concerning the movement of fish cannot be accepted without question, there is no doubt at all that they represent an exceptionally promising line of research. The construction of an apparatus which can be used to measure active metabolism at known speeds is of great importance in itself. Further development of the theory of fish movement, corresponding observations in nature, and experiments conducted under [suitably controlled] physiological conditions, will make it possible to establish the relation between speed of movement and energy expenditures by fish of various sizes. The study of this relationship and the forms which it takes under different conditions can be regarded at the present time [page 183] as the central task in the study of the quantitative aspect of fish metabolism.

Supplement to Chapter IX. When this book was already in press an exceptionally important study was published by Job (1955), carried out in a Canadian laboratory under the direction of Fry. The rate of oxygen consumption of *Salvelinus fontinalis* as related to temperature (5°, 10°, 15° and 20°) and to partial oxygen pressure was studied in detail with a large amount of material and using the unexceptionable flowing-water method. The influence of each of the factors studied was determined using fish--fully acclimated beforehand--of various sizes (from 4 to 1000 g in weight); their effects on the basal metabolism (the lowest metabolism during 24 hours) and on the active metabolism (the metabolism at the maximum possible swimming speed) were both studied. It is unfortunate that it is not possible to give due attention at this time to the important data in Job's thorough work, which would provide important confirmation of many previous conclusions. For example, it is convincingly demonstrated that at all temperatures the dependence of basal and active metabolism on the O_2 content is determined by the metabolic rate, which operates in the same way in fish of all sizes. Job obtained a curve for the relation of metabolism to temperature that is less steep than the one obtained by Graham (see Fig. 18), who used the same species in the same laboratory. However, the deviation from the normal curve of Krogh is not nearly as great as the author believes, basing his opinion on a normal curve which is drawn quite erroneously as a semilogarithmic graph in his figure 4.

Job establishes the relationship of metabolism to size by testing his material by methods that agree fully with those adopted by us, hence his results can be presented most briefly in the form of the k values which he computed by least squares, and a values computed by us from table 1 of Job's work.

	5°		10°		15°		20°	
	a	k	a	k	a	k	a	k
Basal metabolism	0.047	0.856	0.099	0.849	0.138	0.847	0.213	0.802
Active metabolism	0.186	0.942	0.346	0.862	0.406	0.851	0.841	0.750

It is noteworthy that different values of k were obtained at different temperatures, and that at 20° its value agrees fully with our data (equation 6.1.2). [page 184] Job also makes a special study of the relation of routine metabolism to size. It can be seen from his data that basal metabolism comprises 50-60% of the routine metabolism. From this, using equation (6.1.2), a = 0.361; and according to Job the basal metabolism at 20°, expressed in the same units, is 0.213, i.e. 59% of the routine metabolism (see page 107). It is easy to compute the basal and the active metabolism[1] from the figures quoted above, and also the ratio of these two, for each of the temperatures and for various sizes of fish. It turns out that the ratio of basal to active metabolism depends only slightly, or not at all, upon the size of the fish.

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[1] [The text reads "resting metabolism"--obmen pokoi͡a; but, the next sentence shows that this must be a slip.]

Chapter X. [page 185]

The Use of Food for Growth by Fish

1. Introduction

The interests of practical fishery work have directed the attention of scientists to the elucidation of the laws governing the utilization of foods, and of the supplies of food available in a body of water, for the production of fish. The study of the food requirements and the utilization of food by the growing fish is a task for the physiologist. The well-known respiration method, widely used in physiology, zootechnical work and medicine, is one of the main methods for determining food requirements--one which is well formulated and has been repeatedly tested. Pütter and other authors have tested this method as a means of determining the food requirements of fish. In recent years F. V. Krogius and E. M. Krokhin (1948) have computed the food requirements of three-spined sticklebacks and young sockeye salmon in this manner.

This simple and physiologically satisfactory method makes possible rather accurate computations of energy requirements. Of course, this is possible only if the values used in the computations accurately represent the respiration. In order to apply the respiration method it is necessary to know the magnitude of respiration under natural conditions or, in general, under the conditions for which the food requirements are to be calculated.

This is a difficult task and one which, generally speaking, has not yet been solved. It is clear that the average metabolism of fish under natural conditions is higher than the resting metabolism and lower than the maximum active metabolism. Therefore, for sluggish fish the average metabolism under natural conditions is only slightly higher than the resting metabolism, and is close to the routine metabolism calculated from the basic equation. For very active fish the average metabolic rate under natural conditions probably considerably exceeds the resting metabolism and the routine metabolism. Hence, it was difficult to decide in advance how suitable our data on routine metabolism might be for computing the food requirements of fish under natural conditions. However, materials considered later (Chapters XI, XII) [page 186] show that the computed values of routine metabolism can be very useful for estimating fish food requirements. A comparison of the expected values for total metabolism with the rate of growth and the food rations of fish, obtained by quite different methods, made it possible to come close to the average metabolic rate of fish under natural conditions (Chapter XI).

By means of the respiration method it is possible to obtain only the total food requirements and to characterize only the quantitative aspect of feeding. However, the values obtained in this manner are also necessary for an understanding of the qualitative aspects of the processes of metabolism and feeding. The actual significance of any particular qualitative component can only be established if it is possible to learn what part of the general food requirement is supplied by this component. This applies also to any specific peculiarity of metabolism, an appraisal of which is impossible without knowing the quantitative parameters that characterize the various aspects of fish metabolism. "To-day", writes G. S. Karzinkin, "when our country is faced with the task of creating bodies of water for rearing the young of our most valuable food fishes, when thousands of hectares of land not used in agriculture are being converted to fisheries, when we have entered on a path leading to the reorganization of [the life in] our bodies of water and controlling the food supply and the abundance of the fish in them, the question of the quantitative aspect of feeding has acquired a special significance" (1952, page 184). The Soviet scientists whose work concerns the biological foundations of the fishing industry are fully aware of this. In various biological and fishery institutes of the Union work is being carried out aimed at determining the food requirements of fish, finding to what extent food is used for growth, and solving other similar problems. Already much material has been gathered on feeding ratios and daily rations of fish, etc. However, no method yet exists for the study of these questions that has been accepted by all investigators. Often different terms are suggested in order to describe one and the same phenomenon, the same parameters are differently named by different authors, and so on. Furthermore some authors, in their endeavour to procure material immediately useful to fish culture, believe it is possible to curtail their descriptions and make a more or less arbitrary interpretation of experimentally obtained data, without attempting to study them in the light of the principles that have been established in general physiology and zoological technique. It must be said that the results of such purely empirical work are often of very limited value; for it is not clear to what extent the values found for daily rations or other factors can be applied under other conditions or [page 187] to other groups of fish. Practical questions cannot be answered by the accumulation of individual bits of information about feeding ratios, daily rations and other quantitative parameters of fish metabolism, considered separately. That is possible only by a planned study of the general principles of fish metabolism and the nature of their applicability to individual species under different conditions.

When studying the effectiveness of the utilization of food by fish, quantitative indices of the metabolism of growing organisms are involved. It is evident that under these conditions the metabolic rate, as well as other quantitative indices of particular aspects of the metabolism of each fish species, will change more or less, in relation to the stage of development attained. The question of the nature and rate of these changes arises. It is especially important to know how the relationships between the separate aspects of fish metabolism change during development, since these relationships reflect the fundamental direction of the process better than do the changes in each of the indices by itself.

It is well known that the growth of a fish is relatively rapid in the initial stages, and falls off as it grows larger. The metabolic rate changes in a similar way; it too is especially high during the initial stages and it too is inversely related to size. Hence it is clear that in growing fish the rate of food consumption should change even more rapidly with size, for the food meets the requirements both for growth and for metabolism. On the other hand, since both the growth rate and the daily ration [food intake per unit weight] decrease as size and weight increase, the relation between growth and ration, which indicates to what extent food is used for growth, must change less with size; and this is actually observed. Thus when studying the process as a whole, we find it necessary to describe quantitatively at least four different but interlocking aspects: 1) rate of growth, 2) rate of food intake (daily ration), 3) metabolic rate, which reflects the rate of catabolic [dissimilatornye] processes or the so-called energy metabolism, and finally 4) the relation between the growth rate and the rate of food intake, or the extent to which food is used to promote growth. The first three factors are expressed quantitatively in terms of a unit of time, i.e. they are rates, whereas the last factor is a pure number [without dimensions]. When studying changes in these values they must be considered in relation not to age but to size (weight) of the fish, since metabolism and the growth rate of fish are basically functions of size and not of age.

[page 188] Each of the aspects of the development and metabolism of fish mentioned can be expressed, and has actually been expressed, by different authors in different ways and by different terms. Therefore, before we look into the relationship between the growth rate, food ration, metabolic rate and the utilization of food for growth, it must be established what meaning is to be attached to each of these terms and what forms of expression for each of them are most suitable for our purposes.

2. Computation methods for the rate of increase in weight and the food intake of fish

When studying the processes of metabolism and the use of food for promoting growth we are concerned primarily with growth in weight, not linear growth, so everything that follows concerns weight. During the initial stage of the post-embryonic development of fish, during the first days and weeks of growth, the growth rate[1] decreases only very slightly from day to day. For this reason the general picture of growth is close to growth at a constant rate, i.e. the curve of growth in weight is a line concave upward, the separate sectors [uchastki] of which can be expressed well enough by an exponential relationship between weight and age. Therefore, the exponential relationship of weight to age, of which the compound interest formula of weight increase is one form, must be the basis for computations of the average growth rate of young fish during the period of their initial growth. Having made the inexact but unavoidable assumption that during the initial growth of young fish growth proceeds at a constant rate between successive observations, we get:

$$w_n = w_0 e^{kn} = w_0 10^{Kn}$$

where:

k and K are constants, abstract figures that characterize the rate of growth;

n is the duration of the period under study, in days;

w_0 is initial weight;

w_n is weight at the time of observation.

Obviously:

$$10^K = \left(\frac{w_n}{w_0}\right)^{\frac{1}{n}}; \qquad K = \frac{\log w_n - \log w_0}{n}$$

By means of this formula it is easy to compute values for the growth constants, but for our purpose [page 189] it is more convenient and simpler to state the growth rate in the form of

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[1] Here and in all that follows the term growth rate is to be understood in the sense of relative growth rate, i.e. increase in weight during a unit of time divided by the initial weight.

the daily increase in weight expressed as a percentage of the initial weight (C). For one day, when n = 1:

$$\left(\frac{w_n}{w_0}\right)^{\frac{1}{n}} = \frac{w_1}{w_0} = 10^{\frac{1}{n}(\log w_n - \log w_0)}$$

At a constant growth rate the average daily increase in weight (C'_M) during the period of observation equals the percentage increase on any of the days, i.e.:

$$C'_M = C = \left(\frac{w_1}{w_0} - 1\right).100$$

By substituting the observed value of $\frac{w_1}{w_0}$, we get:

$$C'_M = \left[10^{\frac{1}{n}(\log w_n - \log w_0)} - 1\right].100 \qquad (10.2.1)$$

Sometimes this formula is expressed as:

$$C'_M = \left(\sqrt[n]{\frac{w_n}{w_0}} - 1\right).100 \qquad (10.2.2)$$

which is less convenient for computations.

Computation of the average daily [percentage] gain in weight is very simple. It consists of the following: the difference of the logarithms of the final and initial weights is obtained and divided by the number of days elapsed. Then the antilogarithm of the quotient is found, 1 is subtracted, and the figure obtained is multiplied by 100.

The question arises, to what extent is the compound interest equation applicable in cases where--and these occur in practice--the growth rate does not remain strictly constant during the period of observation. Obviously in such situations this method provides only an approximate value for the average daily growth in weight. The practical use of this method of calculation has shown that a satisfactory approximation to the true values can be obtained for the initial period of the growth of young fish. From daily data on the average weight of young carp in the brood ponds of some Belorussian fish farms we had an opportunity to compare the results of a direct computation of the true value of daily increase in weight, calculated from each day's data, with an approximate computation of the same statistic from the initial and final weight, using formula (10.2.1) (Table 21).

[page 190] In our material the daily gain in weight differed greatly between individual days. For instance, in 1951 the extreme values for daily weight gains were 1.0% and 85.8% on the Volma fish farm. Regardless of this, as shown by Table 21, computation by the formula resulted in values that were very close to the true ones in every case.

We have been compelled to dwell on what might seem to be generally understood methods of computing the average daily gain in weight because in recent works many authors have used wrong methods of computing the relative rate of increase in weight of young fish, thereby obtaining results which greatly distort the true picture of the phenomenon (Krivobok, 1953; Tarkovskaîa, 1953; Letichevsky, 1953; Konstantinov, 1953; and others). These authors consider it possible to use the difference between the initial and final weight for computing the average daily values of weight increase, dividing this difference by the number of days elapsed, and to express the quotient obtained as a percentage of the weight of the young fish at the start of the period studied. Obviously the quantity determined in this way (call it c), which these authors erroneously accept as the average weight increase for the period studied, is equal to:

$$c = \left(\frac{w_n - w_0}{w_0 \cdot n}\right) 100, \qquad (10.2.3)$$

where:

w_0 and w_n are the weight of a young fish at the beginning and end of the period of observations;

n is duration of the period [page 191] in days.

By means of the following simple reasoning it is easy to show the unsuitability of this method.

Let us assume that the growth of the young fish proceeds at a constant rate during the observation period so that throughout the entire period the daily increase in weight is 40%. In this event, beginning with an initial weight of 1.54 mg, a day later the weight of a young fish will equal 2.156 mg; when 2 days old it will be 3.018 mg; at 4 days, 5.915 mg; at 6 days, 11.59 mg; at 8 days 22.72 mg; at 10 days 44.53; and so on. This example shows that if the computation method of formula (10.2.3) is used, the "average daily increase in weight" computed from the observations made after two days is 48%, from observations made with a 4-day interval it is 70.7%, for a 6-day interval it is 114.2%, for 8 days, 163.5%; and for 10 days, 279%. In other words for an actually constant daily rate of gain in weight (40%), formula (10.2.3) gives entirely different values that depend on the frequency of the observations. It is clear that this is an unsuitable method, for it can give an entirely distorted impression of the actual growth rate of young fish during the initial period of development. The deviations from the true value when this wrong method is used are the greater, the greater is the growth rate. Therefore, they are especially large during the initial growth period.

In Table 22 the figures obtained by the authors mentioned, using formula (10.2.3) (they call them average daily gains in weight), are compared with the values of this statistic computed from the same data by means of formula (10.2.1). The table shows how greatly these values differ, especially for the rapid growth during the early period of life. Let us remember that the results of computations with formula (10.2.3) diverge the more from the true values, the faster the growth is and the greater the time between observations. Considering that neither the growth rate nor frequency of observations remain constant, they cannot present a true picture of the relative change in the rate of growth. Especially striking are those absurdly high "average daily weight gains" during the initial growth period which create an altogether wrong impression of the possible rate of increase in weight of young fish during the early stages of development, and arise solely from using a wrong method of computation. For example, O. I. Tarkovskaia͡ believes that the average increase in weight of young vobla during the initial growth period is 235%; whereas actually, according to her data, this figure should be close to 58%. This latter rate, of course, corresponds much better to the actual potential for feeding and metabolism at this stage of development.

During later periods of growth, when the weight of fish is fairly large and growth rate is slow, [page 192] it may be assumed that the absolute value of the daily increase in weight remains constant over short periods of time without serious error. This is equal to the difference between the initial and final weight, divided by the duration of the period in days $\left(\frac{w_n - w_0}{n}\right)$. In this case, for an approximation to the true values of average daily weight gain it is necessary that the value for daily gain in weight found in this way be compared not with the initial weight but with the average weight for the period, i.e. $\left(\frac{w_n - w_0}{2}\right)$. Hence:

$$C'_M = \left[\frac{2(w_n - w_0)}{n(w_n + w_0)}\right]100 \qquad (10.2.4)$$

The above methods of computation are used later (Chapter XI) to obtain the average daily increase in dry weight, or in total calorific content, during the growth of fish.

[page 193] Many authors have studied the growth of young fish, of many species. On the basis of the material available, of which examples will be furnished (page 212), it can be seen that during the initial period of growth the daily increase in weight is often 30-40% and even more. As development proceeds and size increases, growth rate inevitably declines rapidly, and in most fish by the end of the first year and during the second year it has sunk to far smaller values, of the order of 1-2% per day, or fractions of a percent. In order to have a clear picture of how high the initial growth rates of young fish are, and the impossibility of maintaining such rates for any length of time, it is sufficient to calculate that with an initial weight of 2 mg and a daily growth of 30%, the tremendous weight of 500 metric tons would be attained in 100 days. The following consideration is no less suggestive: in order to double a fish's weight within 100 days, a steady rate of growth of 0.7% per day is sufficient.

In young fish the expected decline in growth rate as size increases is greatly masked by the very strong influence of temperature, nutrition, and other environmental conditions upon growth rate. As a result, even in series of observations made over prolonged periods, the growth rate of young fish often fluctuates greatly. In such cases the expected decrease in the growth rate with increase in size can be traced only in average data gathered uninterruptedly over rather long periods.

The size of the food ration can also be calculated in various ways. Ordinarily the wet weight of the food organisms is used for computing rations, relating it to the wet weight of the fish. For our purposes the size of the ration obtained by comparing the dry weight of fish and food is more convenient; for when such an expression is used the rations can be compared with the gain in dry weight and also, to a certain extent, with the expenditure of energy in metabolism. This will be dealt with later (page 207).

It is plain that growth rates and rations can be compared only if both values are expressed in the same units. However, that of itself is not enough. It is also necessary to take care that the computation method used for both values, which is always arbitrary to a certain extent, be the same if possible. Much of what was said above regarding computation of mean values for rate of growth can also be applied to the computation of the average ration, if the ration is determined only at the beginning and end of the period studied.

When rations are compared with the weight gains, the ratio between them will differ less from the true value [page 194] than do the two component values. However, this is true only if both indices are computed in a similar manner. Of all the possible ways to express growth rate, for our purposes it is most convenient to use the average daily increase in weight;

for this value can be compared directly with the average daily ration, which is also expressed in percentage of the body weight. This is especially important when it is in terms of percentage of dry weight or of the total calorific content of the body of the fish.

3. Indices of the degree of utilization of food for growth

Two contrasting methods can be employed to express the utilization of food for growth quantitatively. In both cases the starting point is the same: figures for weight increase obtained by one means or another for a particular period of time, and the corresponding figures for the food consumed by the fish. In the first method, the fraction of the food consumed corresponding to a unit of growth in weight is found by dividing the former value by the latter, i.e. figures are obtained which characterize the utilization of food for growth, which are proper fractions and can be expressed as a percentage of the quantity of food consumed. If the weight increase and the food consumed are expressed in wet weight, the utilization coefficient of wet matter for growth is obtained; and similarly for dry weights. When the weight increase and the amount of food consumed are expressed as the weight of nitrogen contained in each, the utilization coefficient for nitrogen is obtained; and when these values are expressed in calories, the utilization coefficient for energy is obtained.

In the second method, we determine how much food is required per unit increase in weight, i.e. figures are obtained which are reciprocals of the coefficients of utilization for growth. The ratio of the wet weight of the food consumed to the gain in weight, also expressed as wet weight (the so-called food coefficient [kormovoĭ koeffitsient]), is most widely employed. This index, the easiest to get in a technical sense, indicates very plainly what amount of food each unit of weight corresponds to. Food coefficients are used to advantage in fish culture in many cases, especially when the fish are fed artificially. However, when applied to an analysis of the laws of growth, the food coefficient is of little use, since its values depend greatly upon the relative amount of dry substance and moisture in the food and in the body of fish; and these, as is well known, can vary within wide limits. Often the ratio of the dry weight of the food to growth in terms of dry weight is also called the food coefficient, [page 195] on a dry weight basis. G. S. Karzinkin, who uses zootechnical terminology, suggests that this ratio should be called the "coefficient of the productive action of food" [koeffitsient produktivnovo deistviia͡ pishchi]. V. S. Ivlev simply calls the ratio of the energy of consumed food to the energy of weight increase the "trophic coefficient". In a wider sense the latter term is used as a synonym of the food coefficient.

When studying empirically obtained data it is important to remember that the values of the utilization coefficients for growth obtained from dry weight, from wet weight, from nitrogen content and from calorific content, together with their reciprocals (the trophic coefficients) will agree better with each other the less is the difference in chemical composition between the food and the fish that use the food. In an ideal case, when the composition of the body of fish and of food is the same, the indices calculated by any of the methods mentioned are all the same.

Of all the possible ways of expressing the relation between growth and food consumption, the one of most interest for our purposes is the energy utilization coefficient, the magnitude of which is close to that of the coefficient of utilization of dry substance when, as often happens, the calorific content of the dry substance of the fish and of its food organisms are similar. Therefore it is quite possible to assume, as G. S. Karzinkin does, that "dry matter represents the consumption of nutrients satisfactorily" (page 268)--though this is true only as a first approximation, and not always.

Because the relation between the processes of growth and metabolism has for a long time attracted the attention of investigators, it is now possible to have some idea of the degree of utilization of matter and energy for growth. At the beginning of this century Tangle and his co-workers established that in the embryonic development of a very diverse assortment of animals, including one fish (fowl, silkworm, Fundulus heteroclitus and frog) the coefficient of energy utilization is close to 0.6, or 60%. This means that toward the end of embryonic development the embryo contains 60% of the initial energy of the ovum (Brody, 1945). Seeing that this applies to a chick as well as to a silkworm, the weight of which at hatching is 50,000 times less than that of a chick, it is evident that this fact establishes an important general characteristic of embryonic growth--namely that, for the most varied types of animals and growth rates, the utilization of the initial supply of matter and of energy in the "food" of the embryo takes place at about the same efficiency. Of course, these data indicate only the approximate mean value of the coefficient of energy utilization during embryonic growth, which may take different values during successive periods of embryonic development. This has been demonstrated for [page 196] the chick, in whose case utilization of energy is more efficient toward the end of development than at the beginning, and approaches 67%. These figures are of interest for our purposes because they can be regarded as the maximum possible values of the use of energy for growth; for it must be assumed that the composition of the "food" of the embryo is close to optimal. From available data, among young fish the efficiency of the utilization of food energy during the initial stages of growth can come close to this maximum (page 212).

Rubner pointed out the systematic relation between growth and energy expenditures during the initial period of postembryonic development. He considered that during the early stages of the postembryonic development, of the most diverse animals, every time the weight is doubled the same or close to the same amount of energy is consumed--namely 34%, on the average, of the total energy expenditure during the period, per unit of weight increase. In his well-known paper of 1924, Rubner made an attempt to extend to fish the views which he first developed with regard to mammals. By using published data on the growth in weight of pike 2 to 9 years old he computed the time required to double its weight. Rubner considered that the calorific content of the body of a pike is 889.2 calories per gram wet weight. He finds the value of the energy metabolism from the conventional size of the body surface, assuming that at 16° fish expend 33.08 Calories per day per [square] dm of surface. To the value thus obtained Rubner adds 26.6% for the specific dynamic action of the food. The sum of the energy equivalent of weight gain, the "energy metabolism", and the specific dynamic action, is taken as the total energy expenditure. Thus Rubner finds that during the first doubling of the weight of pike (from 70 to 140 g) the calorific equivalent of the gain in weight comprises 22.8% of the total energy expenditures; during the time of the second doubling of weight it is 33.1%; during the third doubling, 27.2%; during the fourth, 21.6%; and during the fifth, 14.1%. These values for coefficients of energy utilization are regarded by Rubner as close to those obtained earlier by him for the postembryonic growth of mammals. From this Rubner concludes that the growth of poikilothermal organisms is based upon the same processes as in the case of mammals. Furthermore, he points to the considerably more rapid early postembryonic growth of mammals. For instance, a guinea pig weighing 70 g doubles its weight in 6 days, whereas a pike of the same weight would, in his opinion, require 274 days to double its weight. In order to grow at the same rate as a guinea pig and not use more energy a pike would have to increase its metabolic rate 45.6 times. Actually, according to Rubner's computations, the total metabolism of pike of the weight indicated (0.47 Cal per day) is 43 times lower than that of the guinea pig (20.18 Cal per day).

[page 197] These conclusions cannot be accepted fully and unreservedly for in many ways they are based on indirect and even far-fetched computations. It is known that Rubner's basic data on postembryonic growth of mammals have been subjected to justified criticism. More meticulous computations have shown that there is no reason to believe that the energy expenditures during a doubling of weight are exactly the same for different species, as assumed by Rubner. Furthermore, when the question is studied somewhat more closely, it is difficult to find any uniform computation method for different animals which would be free from a lot of more or less arbitrary assumptions. At any rate the simplification of the actual situation and levelling of the quantitative differences between species in the Rubner structure cannot now be accepted in their original form, let alone the mechanistic ideas regarding the development of organisms on which they were based. However, Rubner's endeavour to demonstrate a regular relationship between growth and metabolism is of definite value. Although coefficients of energy utilization during development cannot be regarded as the same for different organisms, for they seem to differ in a characteristic way in different species, nevertheless these differences are confined within rather narrow limits. A systematic relationship exists between growth rate and metabolism, though it is not as definite and simple as assumed by Rubner. Because of the existence of such a relationship, coefficients of energy utilization are incomparably more stable than metabolic rates or, particularly, growth rates, which for different species and at different stages of development can differ 100-fold.

It is very important that the utilization coefficients, and their reciprocals (the food coefficients), are related to environmental conditions altogether differently from the relationship between rate of growth, rate of feeding (rations), rate of metabolism and environmental conditions. For these latter biological processes, the relation of their rates to temperature does not differ in principle from the relation of metabolic rate to temperature, although there is no complete identity. For instance, although food requirements depend on metabolic rate, the actual ration is related to temperature in a different way than metabolism; because the ration, especially when approaching extremes of temperature, reflects not only the food requirements but depends also upon the difference in foraging activities of the fish at different temperatures, etc.

With regard to the influence of temperature on utilization of food for growth, it not only differs from the relation of metabolism to temperature, but it has an altogether different basis. It has been well established that the utilization of food for growth, considered in its biochemical aspects, [page 198] does not depend at all on temperature within the range of biokinetic temperatures--a matter which I reviewed earlier (Winberg, 1937, pp. 41-44). For a freely-feeding complete organism the matter is more complicated; but even here, it has repeatedly been shown that within the range of temperatures close to the optimum, the utilization of food for growth is practically independent of temperature (Ivlev, 1938; Bily, 1938; Shpet, 1952; Karzinkin, 1952; and others). After considering this phenomenon G. S. Karzinkin writes: "No direct effect of temperature upon [percentage] utilization of dry substance for growth was observed. Here it is a question of difference between stages of development at different temperatures, and [it appears that] the influence of temperature in this field does not follow Van't-Hoff's rule" (page 275). From what has been said above it is clear that neither stage of development nor Van't-Hoff have anything to do with the matter; because Van't-Hoff's rule, if it has some limited applicability to biological phenomena, is useful only in describing the relation of their speed to temperature; it cannot possibly describe the relationships between such phenomena as are involved in the indices of utilization of food for growth.

Although in a biochemical sense the utilization of food for growth does not depend upon temperature over a wide range of the latter, for a freely feeding organism this range is greatly restricted, mostly because the greater the distance from optimum temperatures, the more the actual food consumption lags behind the food requirement. This was beautifully demonstrated for the carp by G. I. Shpet (1952). As a result, degree of utilization for growth is maximal, and the food coefficients are minimal, within the range of optimal temperatures.

Shpet also shows that other factors (oxygen content) affect the value of the food coefficient in the same way, i.e. through the amount of food consumed. It seems that G. S. Karzinkin has the same thing in mind when he says that the food coefficient cannot be identified with the "productive action of the food" [s produktivnym deĭstviem pishchi]. This last term is apparently to be understood here in the sense of the physiological or biochemical utilization of food for growth, although in other contexts the same author gives it a different, wider, meaning.

Thus the degree of utilization of food for growth by freely feeding fish--which is the result of the interaction of the rates of many interlocking processes--in its relation to temperature and other factors is subject, in the first place, to the law of the optimum. In contrast, the concept of a biological optimum cannot be applied directly to the values which describe the rates of the various aspects of metabolism. The maximum size which these values can attain--including the metabolic rate, the size of the ration, the rate of growth, and so on--[page 199] as a rule lie above the biological optimum, and at times they approach the extreme limit of biokinetic temperatures.

4. The coefficients of utilization of food for growth

The important investigations of V. S. Ivlev (1939, 1939a, b, c, 1946, etc.) in which he defines and distinguishes between the concepts encountered in studying the utilization of food energy for growth, are of particular interest. After applying to fish and to other higher organisms, in an appropriate way, modifications of the concepts used by authors who worked with microbiological forms (Terroine, Tauson), Ivlev suggested and used in his work on fish (Ivlev, 1939, 1939a, b, c, 1947) three different coefficients of utilization of energy: those of the first, second and third orders. The coefficient of the first order (K_1) is the relation of the total energy of the food to the energy equivalent of the gain in weight. The reciprocal ratio can be called a "trophic coefficient" if we use the latter term in a broad sense, as Ivlev does.

From his experimental work carried out with several freshwater invertebrates (Infusoria, an oligochaete, mollusks) and young pike, Ivlev finds that about 30% of the total food energy is used for growth during the initial period of development for all the forms studied. He obtained rather interesting data (Ivlev, 1939) when studying the use of food energy for growth by fry of the sheatfish during the absorption of the yolk-sac. With this embryonic type of feeding considerably higher values were found for the energy utilization coefficient--65.7% for the whole period of observation--which agrees well with the data mentioned earlier on energy utilization during embryonic development. It is interesting to note that, according to Ivlev's account, the sheatfish fry were in a state of undulatory motion during the entire period of observation. In spite of this, an energy utilization coefficient was obtained near the upper limiting value, which is in agreement with statements in the literature (Ludwig, 1929; Zeuthen, 1947) that aquatic animals of small size require only a small part of their metabolic energy for movement.

There is no doubt concerning the advisability of using Ivlev's energy utilization coefficient of the first order, or values similar to it, as an easily obtainable index of energy utilization. The basis of all indices of the type [page 200] of the first-order coefficient is the relationship between gain in weight and total food consumed; for example, the relation of the gain in weight, in terms of dry matter, to the dry weight of the food (the reciprocal value is the "productive contribution of the food" [produktivnoe deǐstvie pishchi]). The latter relationship can be called the coefficient of utilization of matter. When the calorific value of the dry food equals the calorific value of the gain in weight then this index does not differ numerically from the coefficient of utilization of energy. Other indices of this type, relating total amount of food to growth, are also in use. For example, G. S. Karzinkin and his colleagues make much use of the ratio of the nitrogen consumed in the food to the nitrogen added in growth during the same period of time.

The Ivlev energy utilization coefficient of the second order is a more significant value, but obtaining it involves meticulous physiological studies in each separate case, which restricts the opportunities for using it.

The energy utilization coefficient of the second order (K_2) is defined in Ivlev's works as the relationship of the food energy to the "total transformed [prevrashchennaia͡] energy", i.e. to the difference between the total energy of the food and the energy discharged in faeces and urine, which difference is usually called "physiologically useful energy". It is plain that only in rare cases, when conducting special research on the nitrogen metabolism of fish, is there a chance to obtain the basic information needed for computing the coefficient of the second order. Furthermore, even if one has data on the excretion of nitrogen in the urine, it is possible to compute only approximately the magnitude of the physiologically useful energy, since no fundamental research has yet been carried out on fish metabolism which would indicate reasonably accurately the amount of energy to which 1 mg of urine nitrogen corresponds.

The following examples of energy utilization coefficients are found in the works of Ivlev (1939, 1939a). For the entire growing season of carp in the second year of life, $K_1 = 31.3\%$ and $K_2 = 41.7\%$.

For young pike after various periods of starvation V. S. Ivlev quotes the following energy utilization coefficients:

Days of starvation	K_1 (%)	K_2 (%)
0	31.5	43.1
10	35.1	46.8
20	38.6	49.7
30	26.0	39.6

[page 201] In order to judge the extent of the utilization for growth of that part of the physiologically useful energy which remains after deducting what is required for "external and internal work", and which goes directly into growth, V. S. Ivlev (1939) suggested an energy utilization coefficient of the third order, and gave an example of the computation of this value for fish. According to him the

total amount of energy consumed as food (Q) represents the sum of the energy of the weight gain (Q'), of the excretions (Q_R), of the internal work (Q_w), of the external work (Q_v) and of the primary heat production (Q_t). $Q = Q' + Q_R + Q_w + Q_v + Q_t$. Ivlev postulates that, in addition to the energy incorporated into the body structure and that used for external and internal work, the physiologically useful energy ($Q - Q_R$) also includes a "primary heat production" which cannot be utilized by poikilothermic organisms. We will not dwell here on the meaning of "primary heat", but will try to see how Ivlev links his concepts with experimental data. He determined the total amount of food energy absorbed by a carp during the growing season, by the nitrogen balance method. In a particular case it was equal to 1829 Cal. The energy of the gain in weight was found by weighing and from determinations of the calorific content of the body of the fish (573 Cal). The energy value of the excreta was computed from the weight and calorific value of the faeces and from the amount of nitrogen in the urine. It was assumed that the urinary nitrogen was in the form of urea (454 Cal). The "internal work" was determined from respiration and the "oxycalorific coefficient" (150 Cal). To establish the "external work" it was assumed that the amount of energy expended by carp in movement was 20% of the "internal work" (30 Cal). Thus all the quantities were found which make up the total amount of absorbed energy, according to Ivlev's concepts, with the exception of the "primary heat". This last quantity was found by difference:
$Q - (Q' + Q_R + Q_w + Q_v) = Q_t$, and it turned out to be very considerable--622 Cal; this amounts to 45% of the physiologically useful energy.

There is a fundamental objection to the determination of "primary heat" from this difference. The entire energy which corresponds to the amount of oxygen consumed was taken into consideration when computing the "external [and internal] work"[1]. The applicability of the first principle of thermodynamics to living organisms has been firmly established by classical 'balance' experiments in physiology. Since this is so, then for aerobic metabolism there is not and cannot be any other source of energy but that which is released by the oxidation of food. Therefore--as is well known--the physiologically useful energy must be fully accounted for by the sum of the energy of weight increase and the energy represented by respiration. In ideally precise balanced experiments and computations [page 202] the difference which Ivlev accepts as

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[1] [The author's omission of "internal" here appears to be a slip.--W.E.R.]

the value of the "primary heat" must be equal to zero[1].

The question now arises, where does the difference come from that Ivlev identifies as "primary heat" in balancing the energy budget for carp? When the observations on the nitrogen balance were being made, respiration was not measured. The necessary values were taken from a previous work by Ivlev (1938), concerning which we noticed earlier (page 100) that in measuring the metabolic rate of carp Ivlev had obtained unusually low values because the measurements were made in winter using greatly exhausted specimens. These particular data were accepted for computing the value of the "internal work", and as a result the latter has a very low value[2]. From table 1 of Ivlev's work, the average weight of a carp was equal to 180 g during the growing season. In this event the rate of consumption of O_2 at 18.5° (the average temperature of the growing season) expected by equation (5.4.1) is 19.1 ml O_2 per hour. If the growing period lasts 2760 hours the oxygen consumption of one fish during the entire season is 52.7 litres; this corresponds to 260 Cal. There is no doubt that this, too, is a great underestimate, if only because metabolic rate does not increase linearly with temperature, and therefore the contribution of the periods of higher temperature will be greater, relatively, than when the computation is made from the "average" temperature. Furthermore, there is no doubt that the metabolism of moving and feeding carp in a pond is considerably higher than the rate of oxygen consumption of unfed fish in a respirometer. In view of these considerations the true values of Q_W and Q_V must be considerably higher than those in Ivlev's work, and the difference $Q - (Q' + Q_R + Q_W + Q_V) = Q_t$ must be correspondingly smaller. Furthermore, we must not forget that the [page 203] total amount of food consumed (Q) was computed from nitrogen metabolism, on the basis of a calculation of the content of the

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[1] In this connection we may note the inaccuracy of V. S. Ivlev's remark that the "true energy productivity of Terroine is not an index of anything", since it invariably comes out as unity. This is true only if the value Q_W is taken to be the entire respiration, as is done by Ivlev but not by Terroine, who by this symbol designates only part of the respiratory metabolism--the "maintenance metabolism", whose magnitude he determines by a special method.

[2] Ivlev indicates that a metabolic rate of 40 mg O_2/kg/hour was used for the computation, and that an "average" carp consumed 42.5 g O_2 during the entire season. For the whole season of 2760 hours, this corresponds to a weight of 375 g for the "average carp", which is about twice as much as their actual average weight during the growing period. This can be seen from table 1 of Ivlev's work.

intestines and analyses of food organisms, i.e. a large number of assumptions and approximations were required. The final result of these calculations can easily diverge from the true [food] consumption by an amount large enough to explain the remainder of the difference under discussion, which as N. V. Puchkov (1954) aptly observed, represents "unaccounted expenditures".

In another work Ivlev (1939b) computes the value of the "primary heat" in a similar way, for young pike reared under experimental conditions. In this case the corresponding difference for the various groups used comprised 39-48% of the physiologically useful energy. In this study the metabolic rate accepted by Ivlev corresponds very well with the values expected for routine metabolism. The values for energy consumption (Q_{w+v}) calculated on this basis were about equal to the "primary heat" determined by difference. To balance the data of the experiment it is enough to make the--highly probable--assumption that the actual mean metabolic rate of the young pike, which were fed with fish fry, was twice as high as the values used in the computation, which latter are close to the resting metabolism. Of course, many other sources of errors could also be responsible for the discrepancy observed.

Ivlev (1939) also computed the elements of the energy balance sheet for sheatfish larvae which were growing at the expense of resorption of the yolk sac. It is very interesting that for this material the "primary heat" proved to be relatively small and comprised only 10% of the physiologically useful energy. From my point of view this means that under the simpler conditions of embryonic nutrition the elements of the energy balance sheet could have been determined with smaller errors.

Thus we cannot recommend using the energy coefficient of the third order suggested by V. S. Ivlev; nor is it possible to accept his further suggestions concerning methods of computing values for "maintenance and productive" energy in fish, or his (1947) standard numbers of carp required for planting [in ponds], since these were worked out using the energy balance sheet for carp described above. These papers, while extremely interesting in their originality of thought and their general approach to the problem, require further improvement and correction.

[page 204] Actually, in his latest work in which the use of food for growth is studied in detail (Ivlev and Ivleva, 1948), a different terminology is proposed, the coefficient of the third order is somewhat modified, and an example of another approach to the experimental determination of this quantity is shown. This work was carried out not with fish, but with young cormorants. However, the terms and methods suggested are of general significance and can be applied fully to fish, consequently we must not overlook them.

The indices which were called coefficients of energy utilization in Ivlev's previous works are now called the "energy coefficients of growth" [energeticheskie koeffitsienty rosta].

In addition they suggest "energy coefficients of work" [energeticheskie koeffitsienty raboty] of three orders; and, using the term in a different sense than formerly, "coefficients of energy utilization" [koeffitsienty ispolzovaniia͡ energii] of two orders. However, no examples of the computation of the latter two indices are given, and it is not explained how this is to be done.

With regard to the "energy coefficients of growth", that is, what were the energy utilization coefficients in the original terminology used above, it can be said that this term, although in some respects more suitable, has its own shortcomings. In the first place, it does not indicate that it does not really concern growth, but rather the use of food for growth. As explained above, the utilization of food for growth can be expressed quantitatively not only by the relation between the calorific contents of the weight increase and of the food, but in many cases the dry weight or nitrogen content can be used to advantage in computations. Therefore I consider it advisable, retaining the basic form of the original term "coefficient of utilization", to use it to describe the utilization of food for growth which can be obtained either on the basis of the relation between the calorific equivalents of weight increase and food, or by using other units to measure these quantities.

The relationship between the food consumed and increase in weight of the young cormorants was studied by the Ivlevs from a direct calculation of the food consumed. An attempt was made to determine the magnitude of that part of the "primary heat" which is associated with plastic metabolism [plasticheskii obmen][1]. The latter value was obtained by deducting the energy of weight increase and the energy of maintenance metabolism from the total amount of incorporated [usvoennaia͡], or physiologically useful, energy. The size of the maintenance metabolism was determined in separate experiments in which the young birds were given a limited amount of food, sufficient only to maintain life and not sufficient for

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[1] [The exact meaning of plasticheskii in this context escapes me; perhaps "muscular" would come close. In species descriptions, plasticheskii is used in the general sense of morphometric--as contrasted with meristic.--W.E.R.]

growth. It is easy to see that this method of determining the "primary heat" is based upon the hypothesis that the "external and internal work" in normally feeding and growing fledglings does not differ from [page 205] the corresponding values for young birds that receive insufficient food. If however in normally growing fledglings the "external and internal work" is greater than in hungry ones, then there is no reason to ascribe the indicated difference entirely to "primary heat". Consequently, the difficulties in determining the "maintenance metabolism" and the approximate nature of this quantity make it impossible to assume that the "primary heat", and therefore also the food-utilization coefficient of the third order, can be given a sufficiently definite quantitative expression.

In contrast to this, the coefficients of food utilization of the first and second orders can be determined with the requisite degree of accuracy and have very wide applicability.

The Ivlev coefficients of the first and second orders and parameters similar to them do not exhaust the possibilities for quantitative expression of the utilization of energy for growth. For example, G. S. Karzinkin makes use of the percentage weight increase not only as compared to the total amount of food, but also to the amount of food absorbed [resorbirovannaîa]. In some situations this is fully advisable, especially when studying the use of dry substance or nitrogen for growth. In an analogous manner it would also be easy to obtain an energy utilization coefficient that would, as it were, occupy an intermediate position between the Ivlev coefficients of the first and second orders.

In the same way, too, Ivlev (1939) in one of his studies on the utilization of fat and carbohydrates by carp, cites the "coefficients of utilization" of fat and carbohydrates, obtained by a special method of computation; but they have an altogether different meaning than the coefficients of the first and second orders which resemble them in name.

Thus, at present, various quantitative indices are used for appraising the degree of utilization of matter and energy in food for growth, which are often called by the same or similar names. To avoid possible misunderstandings, one must differentiate strictly between at least three methods for computing the relationship between growth and food requirements, or three categories of indices of utilization of matter or energy for growth. In the first case the indices are computed from quantities that are proportional to the total amount of food consumed--the Ivlev coefficients of the first order; in the second case they are computed from the amount of food absorbed (the total minus what is ejected in the faeces). In the third case, which is applicable to the relationship between energy of growth and of food, the value for growth is compared with the physiologically useful energy (the energy of the food absorbed minus the energy lost in the urine)--the coefficient of energy utilization of the second order. We should observe that only in the case of proteins does the energy of food absorbed differ from the physiologically useful energy.

[page 206] The first form of the relationship between growth and food, i.e. values of the type of Ivlev's utilization coefficients of the first order, suffices for our purposes. In practice, there are very few situations where it is possible to learn the calorific value of the weight increase and of the food. In addition, therefore, one must use the relationship between the dry weights of the growth and of the food (the coefficient of utilization of food for growth), which, to a first approximation, describes the energy relationship sufficiently well in most cases.

Chapter XI. [page 207]

Growth Rate and Metabolic Rate of Fish

1. The interrelation of growth rate, food rations and metabolic rate (the balanced equation)

Thanks to the fact that growth rate, food rations and metabolic rate are strictly and definitely inter-related, it is possible, if one knows two of these values, to compute the third. The rate of food consumption must meet the needs of growth and metabolism, i.e. when expressed in equivalent units it [food] must vary proportionally to the sum of the two last-named values. In computations it is most accurate to express all three indices in energy units, as is customary in physiology.

The sum of energy expenditures for respiration and growth does not equal the total energy of the food, but only the so-called physiologically useful part of it, i.e. the difference between total energy and energy given off in excrement and urine (Tomme, 1949). Rations are computed from the total amount of food. Therefore, one must know how the total energy of food is connected with expenditures for respiration and growth.

The ratio of physiologically useful energy to total energy can vary, depending on kind of food, species of fish, stage of development and other conditions. However, we may conclude from the studies of the assimilability [usvoi͡aemost] of food by fish (G. S. Karzinkin, 1952) that these differences are to be located within relatively narrow limits in most cases. Therefore, it is relatively easy to establish what part of the total food energy, on the average, is ejected in the excreta when fish feed upon natural foods. In table 31 of Karzinkin's book are gathered together data on digestibility [perevarimost] of the proteins of different food organisms, obtained by Mann, Yablonskai͡a and other authors for 10 different species of fish. The values quoted in the table fluctuate between 76.0 to 96.6%, and they show no clear relationships with kind of food or with the species of fish that used it. It seems that these differences reflect, to a very considerable extent, the inevitable random fluctuations in experimental results. Karzinkin, not considering this possibility, is inclined to consider that all the differences, even the small ones, [page 208] are associated with peculiarities of the different species. Nevertheless, he writes that: "On the whole, comparative material concerning a number of fishes makes it possible to conclude that digestibility of proteins is very much the same for a number of species. Such agreement makes it possible to compute the content of digestible proteins in a food supply from knowledge of their digestion by any single species of fish. The error in applying such results to other species of fish will be within the range ±5-6%." On the average for the 43 values in table 31, digestibility of protein is equal to 88.4%.

The digestibility of food computed on the basis of dry weight or calorific content can differ from its digestibility with respect to nitrogen, but for most natural foods the difference is small. According to E. A. Yablonskaîâ's data for carp, quoted in table 27 of Karzinkin's book, the average digestibility for 18 species of food organisms (mollusks weighed together with their shells are excepted) is as follows: on a dry weight basis, 84.7%; on the basis of calorific content, 84.0%; and on the basis of nitrogen, 90.0%. In this case, as in many others, digestibility on a dry weight or calorific basis is somewhat lower than with respect to nitrogen.

Judging by the aggregate of data on hand we will not be far wrong in assuming that under natural conditions the digestibility of natural foods averages 85%.

It is considerably more difficult to get an idea of what part of the total energy of the food is secreted in the urine. Even in cases where the nitrogen content of the urine is known this is not altogether clear. V. S. Ivlev (1939) assumes in his computations that "in the carp, nitrogen is given off primarily in the form of urea". N. V. Puchkov (1954) writes that the final product of albuminous metabolism in bony freshwater fishes consists of "urea and ammonia; but ammonia greatly predominates" (page 156). The more ammonia predominates over urea in fish urine, the less is the energy corresponding to a unit of nitrogen secreted, as compared with the amount inserted in the corresponding computation when urea is the main product of protein metabolism.

If all the nitrogen of protein metabolism is given off in the form of ammonia, then the physiologically useful energy becomes equal to the digestible energy.

First of all we will see what the values would be if urea were the main product of protein metabolism. It is well known that in this case the total energy of 1 g of protein is considered to be close to 5.7 Cal, and the physiologically useful energy about 4.1 Cal. Thus the energy loss in the urine comprises 28% of the total energy of the protein. When the entire protein in the food is used up in energy metabolism, which could occur only if there were no growth, the loss of energy in urine will be a maximum. In food of ordinary composition not more than [page 209] 50% of the total energy is in the protein. In such case, if there is no growth at all, 14% of the energy of the food absorbed will be lost in the urine. If 50% of the protein is used for growth then the loss in urine will amount to only 7%. If only 50% of the nitrogen excreted in the urine occurs in the form of ammonia, then the energy loss observed should again be reduced to half, and we get 3.5% of the energy of the food absorbed, or 3% of the total energy in the case of 85% assimilability. Even this tentative and approximate computation shows convincingly that the loss of energy in the urine, especially in the case of growing fish, cannot comprise a large part of the total food energy under normal conditions.

On this basis it is accepted in all further computations that total loss of food energy in excrements and urine, when the fish are fed natural foods, comprises 20% of the total food energy, or in other words that the physiologically useful energy comprises 80% of the total energy of the ration.

If the physiological food energy comprises 80% of the total, it is evident that the second-order coefficient of utilization of food can easily be obtained from the first-order coefficient, because then $K_2 = 1.25\ K_1$. For example, if the first-order coefficient is 30%, then the second-order coefficient will be 37.5%.

It is now easy to write a balanced equation which relates metabolic rate, growth rate and the rate of food intake (the ration), which will make it possible to compute the third value from any two known values--for example, to find the size of the ration from the metabolic rate and the growth rate. It is clear that all three members of the equation must be expressed in the same manner and referred to the same time unit, for which, when studying the growth of young fish, it is most natural to use the 24-hour day. The basic balanced equation can be expressed in writing as follows:

$$\text{Energy of weight increase} + \text{energy of metabolism}$$

$$= \text{physiologically useful energy}$$

$$= 0.80(\text{energy of the ration})$$

Or: Energy of the ration

$$= 1.25(\text{energy of metabolism} + \text{energy of weight increase})$$

For an ideal case it is easy to express rate of respiration in the form of expenditure of dry substance for metabolism. In fact, if the calorific equivalent of dry substance is 5000 cal/g, then the consumption of 1 ml of oxygen, which is equivalent to the release of 5 cal of energy, means the expenditure of 1 mg of dry body substance in metabolism. When applied to actual data, such a method of expressing the metabolic rate can only be sanctioned for approximate computations of a general nature, seeing that it contains inaccuracies which become more serious the more the calorific equivalent of the dry substance of the fish's body differs from 5000. However, since only in rare cases is it possible to have access to data expressed in energy units, the method just given--computing the expenditures in metabolism in terms of dry weight--can be [page 210] very useful, especially if one constantly keeps in mind the possible sources of error and knows the range of possible deviations from the true values.

On this basis it is permissible to present the metabolic rate in the form of "expenditures for metabolism" expressed as a percentage of weight. If 1 ml of oxygen consumed corresponds to the expenditure of 1 mg of dry weight, then from the size of the metabolic rate $\frac{Q}{W}$ expressed in the ordinary form (ml O_2 per g of wet weight per hour), the expenditures for metabolism per day, as percentage of the dry weight, can be obtained from the formula:

$$\text{Expenditure for metabolism per day (as percentage of weight)} = \frac{(\text{consumption of } O_2 \text{ as ml/g wet weight/hour}) \times 240}{\text{content of dry substance in \%}}$$

When it is possible to assume that the calorific equivalent of the dry substance of the body of the fish and of its food are the same, the balanced equation takes the following form:

$$\text{Increase in dry weight} + \text{expenditure of the dry substance for metabolism} = 0.80(\text{dry substance of the ration})$$

This expression is identical with the above relationship between energy equivalents only in the "ideal" situation when the calorific value of the dry substance of the food and of the fish are the same; in other situations it is only an approximate equation. Nevertheless, as shown below, its application to concrete data on the growth and the feeding of young fish has been very fruitful.

In principle, the computation on the basis of calorific equivalents is more accurate. In practice, however, in the first place one seldom has the necessary values at one's disposal, and in the second place, even when the calorific equivalents are known they are usually not obtained by direct combustion in a calorimetric bomb, but indirectly from computations that are commonly made on the basis of dry weight and nitrogen content--computations which contain a number of more or less arbitrary postulates. Sometimes in determining calorific equivalents recourse is had to various forms of so-called wet combustion, which also is an indirect method and can lead to large errors (see page 211). Therefore, although in principle the computation using weight units for growth and for the ration is considerably less accurate, nevertheless in practice it is necessary to resort to it; and it is often difficult to say which leads to the smaller error: to use accurately determined figures for the dry weight, or calorific equivalents that have been obtained by indirect methods involving many approximations.

When calculating from dry weight, one is inevitably compelled to ascribe, more or less arbitrarily, a definite calorific value to 1 g of dry weight. The greatest errors arise from the facts that [page 211] firstly, the calorific equivalent of the dry substance in many cases does not really remain constant, but changes during development or with the seasons, and secondly, the calorific equivalent of the dry substance of different species differs. Nevertheless, approximate computations on the basis of dry weight are permissible because the calorific equivalent of a dry-weight unit in many cases varies far less than that of a wet-weight unit, which depends on moisture content and differs in different species and at different stages of development.

For the tentative computations to follow it is taken that the calorific equivalent of 1 gram of dry weight of the body of the fish, and of its foods, is equal to 5000 gram-calories. The following data give an idea of the extent of the possible deviations from the true values. By means of direct calorimetry Rubner (1924) showed that the calorific equivalent of the ash-free and fat-free organic substance of the body of a crucian carp is equal to 5347 cal per gram of dry weight; for bream it is 5317 cal; for pike, 5283 cal; and for tench, 5391 cal. According to these data the mean calorific equivalent of fat-free substance is 5309 cal per gram dry weight. It is evident that the calorific equivalent of the [actual] dry substance will tend to be below this value by reason of the ash content, and will tend to be higher by reason of the fat content. Let us assume that the calorific equivalent of 1 gram of fat is 9500. If the calorific equivalent of 1 g of the dry substance be indicated by q, the percentage of ash by s, and the percentage of fat by f, then:

$$q = \frac{5300(100-s)}{100} + \frac{4200.f}{100} = 5300 - 53s + 42f$$

It is easy to compute by how much the calorific value will be reduced when computed, not on the ash-free, but on the ordinary dry weight basis. The usual ash content in the body of a fish does not exceed 5%. If there is no fat at all, the calorific content of the dry weight will be 5035. From the above considerations, it is impossible to understand why the calorific equivalent of the dry substance of the fish's body has been assigned such low values as have at times been quoted in the literature, when calorific values were determined by inadequately tested indirect methods. For example, in table 97 of the book by G. S. Karzinkin (1952) data are presented concerning the calorific equivalent of the dry substance of the body of roach, which at the beginning of summer are assigned values close to 3750 cal/g dry weight. It is easy to see that so low a calorific value corresponds to an ash content of 29% even in the complete absence of fat. This percentage exceeds the ash content of the bones of fish.

Obviously the calorific equivalent of dry substance increases as fat content increases. For example, at an ash content of 5%, and a fat content of 10% (which is a rather large amount for a freshwater fish), the calorific equivalent of the dry substance computed by the above formula will be 5450. According to Ivlev's (1939) data, during the second year of growth [page 212] the calorific equivalent of the dry weight of the body of carp increases from 4310 to 5573 cal/g dry weight, i.e. it differs from 5000 by from -14% to +12%. It would seem that the difference in calorific value of the dry weight of the body of carp, as between the start and the end of the [growing] season, approaches the maximum possible; this is the difference between yearlings much exhausted by wintering-over, and fat autumn two-year-olds. Differences in the calorific equivalent of young fish during the initial stages of growth are possible only within considerably narrower limits. For example, it can be seen from Krivobok's (1953) data that the calorific equivalent of young wild carp fluctuated irregularly within the range 4500-5030 cal/g during the period May 26 to August 14. Nevertheless, it must be admitted that the results of computations based on the provisional assumption of a constant calorific equivalent for dry weight of 5000 cal/g can deviate from the true figures by ±20%.

2. The relationship between growth and metabolism of various species of fish, from data obtained by the method of nitrogen balance

In recent years Soviet investigators, primarily G. S. Karzinkin and his students, have carried out a series of experiments in which they studied food rations during growth of the young of a number of species of fish. During this research the size of the ration was arrived at either by direct computation of the food required, as is possible when the young fish are raised in the laboratory, or by the indirect method of the nitrogen balance. This method was first described in 1937 in a work by five authors (Meĭen, Karzinkin, Ivlev, Lipin and Sheina), based on the results of some experimental work done by V. S. Ivlev and described by him in detail in his 1939 paper. In subsequent years Karzinkin and his students have used the nitrogen-balance method extensively. The nitrogen-balance method is of particular interest because the figures obtained using it represent the metabolism of the fish under natural conditions. Therefore a comparison of these data, which are completely independent of the basic equation, can serve as a check on the reality of the generalizations made and the possibility of estimating fish metabolism from them under natural conditions. Furthermore, by using the abovementioned concepts and methods of computation, it is possible from such materials to trace how the interdependence of the processes of growth and metabolism works out in different fish and under different conditions. As a result, this will help to clarify to what extent the data on fish respiration could be used to solve the question of food rations for fish under natural conditions, which is important for the fish-rearing industry, and to develop reliable methods for determining these quantities.

[page 213] We will illustrate the method of computation by a concrete example, using data from the thorough and meticulous work of M. N. Krivobok (1953), who studied the feeding and growth of young wild carp in a hatchery of the Volga delta. Krivobok applied the method of nitrogen balance, and from the values obtained he computed the amount of nitrogen consumed by the fish per day for each of the periods of observation. It has been shown repeatedly that the nitrogen content of the dry substance of various food organisms deviates little from 10%. Therefore we consider it possible to obtain the dry weight of the food consumed by multiplying the weight of the nitrogen consumed by 10. For example, during the period July 14-28, 4.085 mg of nitrogen per day are required for one fish, according to Krivobok's data. Therefore, during this period 40.85 mg of food (dry weight) were required per day. During this period the average dry weight of a fish amounted to 498.4 mg. Hence the daily ration, expressed as percentage, is 8.2%. We may notice that daily rations have been computed by Krivobok and other colleagues and students of G. S. Karzinkin in a more complex manner. They take into consideration the species composition of the organisms consumed, their weight, and the relative nitrogen content of each food component. In the work under consideration the rations were obtained in this way. Comparing them with our data, it is easy to see that the differences are small and random. In 5 instances our method of computation yielded somewhat lower values, while in 3 instances they were higher. The relative nitrogen content in each of the food objects can vary over a rather wide range. Therefore these more complex computations, which take into consideration the composition of the food, the different nitrogen contents of the different food organisms, etc., result in only a fictitious precision in many instances.

It is important to know what method is used to compute the size of the daily increase in weight and the daily ration. It was shown above (page 190) that Krivobok, as well as other authors, have used an inaccurate method of computing the average daily increase in weight. He also used linear interpolation to compute the average daily food consumption for a given period of observation; that is, the arithmetic mean of the quantities consumed at the beginning and at the end of the period, divided by the duration of the period in days, was regarded as the average amount of food consumed. However, in this case, in converting from absolute to relative values, the ration was expressed as a percentage of the average weight for the period (the arithmetic mean of the initial and final weight) and not as percentage of the initial weight (as was done when computing the daily increase in weight). Although in the case of rapid growth it is impossible to obtain completely accurate values in this way, nevertheless the unavoidable difference from the true [page 214] value will be considerably less than when the percentage is calculated from the weight at the beginning of the period. However, it is most important that when the mean percentage increase in weight for the period is computed in the same way, that is, in terms of the initial weight rather than the mean weight, the ratio of the average weight increase to the average ration will for practical purposes not differ from the true value, though the [absolute] difference between them will differ somewhat from the true difference. For this reason we have considered it permissible not to refer all quantities to the basis of the initial values, which in any event are not always published, but have taken care only to see to it that the percentage growth in weight and the relative daily ration are computed in the same way and are compared with the mean weight for the period. Nevertheless, it should be borne in mind that Table 23 and those that follow show quantities for growth and for rations which, strictly speaking, are only approximate average growths and rations for the periods in question. However, their deviation from the true figures can only be detected during the periods of the most rapid growth.

The computation of the coefficient of utilization does not require explanation, since it is simply the quotient obtained by dividing the daily weight increases by the daily rations.

The balanced equation makes it possible to compute a third quantity by means of two known quantities. From Krivobok's data the rations and the weight increases are known. Therefore from these data the "expenditures for metabolism", i.e. the mean metabolic rate of the fish used in the experiment, can be computed from the balanced equation. Let us remember that the special interest of values for metabolism computed in this way consists in the fact that they should represent the mean metabolic rate under natural conditions, [page 215] since Krivobok's material refers to the growth of fish under natural conditions.

"Expenditures for metabolism" have been computed from the balanced equation in the following way. In our example, for the period July 14-28 the ration was 8.2%, and the gain in weight was 0.96%. Hence the expenditures for metabolism were:

$$0.8 \times 8.2 - 0.96 = 5.6\%$$

Let us recall that if the calorific equivalent of dry substance is 5000 cal/g, then 1 ml O_2 corresponds to the metabolism of 1 mg of the dry substance. Therefore, at the 5.6% level of expenditure for metabolism, 1 g of dry substance requires 56 ml O_2 per day. According to Krivobok, during the above period the bodies of these fish included 19.4% of dry substance. Hence we can calculate that for 1 g of wet weight of the fish, $56 \times 0.194 = 10.9$ ml O_2 are required every day, or 0.45 ml O_2 per hour.

The expected values for metabolism (column 9, table 23) were computed, as usual, on the basis of the wet weight of the fish from the basic equation (7.3.3), and were reduced using Table 1 to the indicated mean temperature of the period of the observations. For example, for the period July 14-28 the expected value of routine metabolism at an average fish weight of 2.566 g is 0.25 ml O_2/g/hour at 20°, and it is 0.37 at 24.7°. Krivobok's article also contains results of measurements he made on the rate of oxygen consumption, which are shown in the last column of Table 23.

Let us now study Table 23, the first three and last columns of which contain Krivobok's data, the others being calculated by the methods stated. Table 23 shows, as would be expected, that the daily weight gains and rations, which were high at first, decrease rapidly, whereas the utilization of food for growth remains for a long time at almost the same high level as prevailed during the initial period. There is no doubt that the rapid reduction of the values for the daily growth, which begins on June 26, and is accompanied by decrease of the utilization coefficient, reflects a deterioration of feeding conditions, because carp of these sizes are capable of growing rapidly and maintaining high values of the coefficients of food utilization.

The last three columns of the table are of greatest interest: they contain figures for metabolic rate computed from daily weight increases and rations using the balanced equation (column 8), expected values of routine metabolism obtained from the basic equation (column 9), and measurements of respiration made by Krivobok (column 10). Inspection of the table reveals that the three series of values are surprisingly close. Considering the many approximations and possible sources of error, this result [page 216] is of exceptional interest. Of course the almost complete agreement of the figures for metabolic rate obtained in three different and independent ways can be accidental to some extent. Nevertheless, even if so close an agreement of the values computed in different ways is not regarded as typical, it must be admitted that even with the largest possible degree of error the disagreement among these values could not become very great. This leads to some important conclusions. Firstly, the result of the computation can serve as a convincing practical demonstration of the usefulness of the methods used in our tentative comparisons of the magnitudes of metabolism, growth rate and food rations among growing fish. Further, we must conclude that the metabolic rate of young carp of these sizes, under natural conditions, is close to the routine metabolism of fish [in general], which would be possible only if there is relatively small expenditure of energy for movement.

Let us now take an example of quite a different character referring to 4th-year [chetyrekhletnye--i.e. age 3+] roach of Lake Glubokoe [Deep Lake], whose nitrogen balance has been studied by G. S. Karzinkin (1952). The studies lasted 3 months, from the end of May to the end of August. Seven times during this period the nitrogen balance of fish caught in the lake was determined, as was the composition of their food (from the contents of the digestive tract, etc.). The results of the study are presented in three tables in Karzinkin's book (tables 97-99). In detail, these tables contain values calculated by Karzinkin indicating how many "Calories were eaten during each period", and the calorific content of the body of the fish. This makes it possible to use as the basis for our computations not the dry weights, as was done in the previous [page 217] example, but rather to use the calorific equivalents of weight gains and rations directly. Apart from that, all the computations are completely analogous to those described above. In this example, underlying all the data on the utilization of food for growth there is the assumption that the average weights of the fish caught at successive intervals represent the growth of the fish in the lake. The weight of the fish increased from 19.6 to 25.8 g during the period from May 26 to August 26. With such slow growth, when the weight increases for half-month periods are obtained from differences between the weights of fish caught in the lake it was, of course, impossible to avoid accidental and irregular fluctuations in the computed growth rates; in fact, even negative values for growth were obtained for one of the periods. Hence there is no reason to expect consistency in the fluctuations of the values from sample to sample; rather, they must be viewed as a whole for the entire period of observation. Notice [in Table 24] the small daily growth--0.54% on the average. The mean daily increase in wet weight is even less--only 0.24%. The increases calculated on the basis of the calorific equivalents are somewhat larger because the calorific equivalent of the body of the fish increased from 3747 to 4315 cal per gram of dry substance during the period of observation. We observe also that the daily increases computed by Karzinkin on the basis of nitrogen content have about the same values as those which we have computed on the basis of calorific equivalents. In spite of the fluctuations in the K_1 values for successive periods, which are plainly random, it is clear also that the effectiveness of utilization of food for growth by roach in Lake Glubokoe is small. Computed from the mean values for daily growth and food intake, the coefficient of utilization is 11.3%.

The metabolic rate is calculated by multiplying the percentage expenditure for metabolism by the mean calorific content of the body of the fish for each period and dividing the result by the mean wet weight of fish, then by 5 to change from calories to ml O_2, and by 24 to change from days to hours. In this case the computed values of the metabolic rate (average, 0.28) are about 1.5 times the values for routine metabolism expected from the basic equation (average, 0.18). No matter what this difference may be due to--unaccounted-for energy used in movement of the fish, or simply errors in the experiments or computations--it must be regarded as a small one, especially if we consider that when average growth is small, many of the sources of the error in the nitrogen balance method are greatly magnified.

Table 25 contains data for pond carp in their second year of life, from the results of the first experiment in which the nitrogen balance method was applied to fish (V. S. Ivlev, 1939). These data are also contained in tables 91 and 92 of Karzinkin's book. In this case, as in the previous one, it was possible to make the computations on the basis of calorific equivalents [page 219] of the weight increase and of the rations. The rations were obtained from the nitrogen balance (table 92 of Karzinkin). It was assumed that 1 mg of nitrogen in the food is the equivalent of 50 cal of energy. The values for weight increase were obtained in the manner explained above, which is the same as the method used by Karzinkin. The table shows plainly that in the case of carp, in contrast to more slowly growing fish, both the rations and the degree of utilization of food for growth remain very high even when the body weight is quite large.

The last two columns of the table show that the values computed for the metabolism are approximately 2.5-3 times higher than expected. So large a discrepancy cannot be a result of inaccuracies in the computations. The data on hand for the nitrogen metabolism show that the assumption made, that the physiologically useful energy comprises 80% of the total energy, agrees with the actual relationship of these values fairly well. The daily weight increases are computed directly from the increases for the separate periods, and cannot differ greatly from the true values. Neither can it be supposed that the daily rations obtained from the nitrogen metabolism data are greatly overestimated, since the actual magnitude of the energy utilization coefficients cannot be appreciably larger than the high values quoted in the table. Therefore we must come to the conclusion that under natural conditions the metabolism of actively feeding and rapidly growing second-year carp is at least twice the expected level of routine metabolism.

A similar conclusion is derived from the thorough work of E. A. Yablonskaia͡ (1951) on the nitrogen balance of the verkhovka. Table 26 contains data obtained during the post-spawning period, when the changes in weight depend only upon growth. As was to be expected for mature verkhovka, not only are the daily weight increments very small but the food utilization coefficients are also. The last columns of the table contain data on the metabolic rate. Notice first that, again in this example, the expected values for routine metabolism agree exceptionally well with the results of measurements of rate of oxygen consumption made by Yablonskaia͡ directly on the material used in the experiments. However, the metabolic rate computed from the basic balanced equation was 2.0-2.8 times the one measured. Here too, neither the various possible variants of the method of computation, nor their inevitable errors, could lead to so great a divergence of the computed values for metabolic rate from those expected and measured. Such a difference could arise if the rate of nitrogen excretion were higher under laboratory conditions than under natural conditions, or if the rate of uptake of oxygen under the conditions of the measurements [page 221] were lower than the rate of oxygen consumption under natural conditions. For the carp, evidence has already been adduced for the second proposition. In the present example such direct evidence is lacking, and there is no reason to assume, without further study, that laboratory data on nitrogen metabolism always accurately reflect the metabolic rate under natural conditions. Bearing in mind other examples, and also the fact that under natural conditions the metabolic rate must be somewhat higher than the routine metabolism, it is logical to conclude that the difference observed results from this cause to a considerable extent. If this is really so, then the computations made from the basic balanced equation indicate that the nitrogen-balance method provides data that represent, accurately enough, the quantitative side of the metabolism of fish living under natural conditions.

3. The relationship of the processes of growth and metabolism in fish, from direct computations of food consumption

In addition to material obtained by the nitrogen-balance method, we can also use data concerning the food ration of the young of various fishes, obtained by direct computation of food consumption. Data of this kind are contained in G. S. Karzinkin's book, concerning young inconnu, sturgeon and pike. Estimating a ration by direct computation of the food consumed has, at first glance, all the advantages of a direct approach. In practice, many difficulties of a technical nature limit the possibilities of this method. It is for good reasons that Karzinkin prefers the nitrogen-balance method. In addition to the technical difficulties, the method of direct computation of food consumption is applicable only to fish that are being raised under the artificial conditions of a laboratory experiment. Nevertheless, it is interesting to know what figures for metabolic rate will result from data obtained by a method other than the nitrogen-balance method.

Tables 51 and 83-90 of Karzinkin's book show the results of experiments with inconnu. Of these data, we will use the material that applies to the young fish raised at the temperature closest to 20°, i.e. 18.5-19° (Table 27). As usual, during the earliest period of growth we observe large daily weight increases and rather effective utilization of food for growth (K_1 = 40-60). In spite of some fluctuation of the individual figures, the computed metabolic rates in this case are in general very close to expected values for routine metabolism.

[page 222] The results of a similar experiment with young osëtr were used by Karzinkin for the various computations presented in his book in tables 45, 66, 67, 70, 75, 81 and 82. From this material our Table 28 has been put together in the usual way. The "approximate" daily weight increments of the young sturgeon used in the experiment are not very great. The true daily increases for the first 4 growth periods are 16.5, 15.1, 13.1 and 8.9 respectively. We note the reduction in the daily increases as growth proceeds, and the low value for the increase during the last period of observation. In spite of the reduction in growth rate, the coefficients of energy utilization had not decreased up to the end of the experiment; their continued high level is apparently characteristic of [page 223] this species, which has a prolonged period of growth and large definitive size. As shown in the last two columns of the table, the metabolic rate computed from the balanced equation is 1.6-2.1 times the expected values for routine metabolism during the first four periods of observation. Only during the last period was the calculated figure for metabolism somewhat less than the expected figure. It is difficult to say whether this reflects a lowered metabolic rate during the last period of the experiment, of fish that were being raised under artificial conditions, or whether it is simply due to an error in determining the daily ration for this period.

In his table 42 Karzinkin gives the food rations for young pike, one part fed on daphnids, the other part on young roach. The usual computations lead, in this case, to an unusual result (Table 29). According to Karzinkin's data, pike raised under the conditions of the experiment described had very high food rations though their growth rate was relatively slow; but the expenditures for metabolism were unusually large. The percentage of expenditure for metabolism, computed from these data, is 69%. Correspondingly, [page 224] the percentage utilization of food is unusually low during the initial growth period, a time when usually not less than 50% of the food is utilized for growth. In this instance, however, whether the food was Daphnia or fish fry, K_1 lies within the range 20-25%. This is perplexing in itself: such values of K_1 could occur as a result of insufficient food, but this explanation is precluded by the very high rations, which are in keeping with the high metabolic rate, 4 to 6 times the expected rate. In this case there is no doubt that errors and inaccuracies have crept in during the conduct of the experiment or in making the computations, especially during the first periods of observation, so that food rations were computed that are much higher than the true ones. Consequently the figures for metabolism of young pike computed from these data cannot be regarded as reliable. The comparisons made are of considerable interest in another way. They demonstrate a sort of byproduct of using the balanced equation--the possibility of using it to judge the reliability of quantitative data on metabolism obtained from individual experiments.

* * *

Our comparison of the metabolic rates expected from the average results of measurements of fish respiration, with independent data on growth and food, has had very encouraging results. In spite of many approximations and possible sources of errors, the computed figures for metabolism agree quite well with the expected and possible values of the metabolic rate in all cases, except the obviously unreliable data of the last example concerning the growth of young pike. In no case was the computed figure for metabolic rate smaller than the expected rate of routine metabolism. We recall that the computed value was about 1.5 times the expected routine metabolism in the case of the fourth-year roach from Lake Glubokoe; for second-year carp that were feeding intensively and growing rapidly it was 2.5-3 times; for mature verkhovka, 2.0-2.8 times;

and for young osëtr, 1.5-2 times. However for fingerling wild carp and inconnu the calculated values for metabolism were very close to the expected values for routine metabolism. It may be no accident that the calculated values for respiration were close to the routine metabolism in the two examples that pertain to the initial period of growth. Possibly when the oxygen consumption rate [page 225] of fry of minimal sizes is measured by the usual methods, values are obtained that correspond more closely to the mean metabolic rate under natural conditions than in the case of larger fish. This might be associated, for example, with the fact that when fish larvae and small fry are transferred to respirometers in which they can move about freely, there is less disturbance of their normal behaviour.

However, much remains to be explained, and the material at hand is not free from a number of contradictions. For example, in the case of young osëtr, the computed values were higher than the expected values even in the initial growth periods (Table 28). On the other hand, agreement of the computed and expected values of metabolism, etc., is observed in carp not only in the earliest stages, but also in young of 2.5-3 g (Table 23).

Further research is necessary, which should not stop at the empirical accumulation of experimental data, but should be based on definite hypotheses concerning the association between the nutrition, growth and metabolism of fish.

I believe that the attempt made here to survey the heterogeneous data on the metabolism of different fishes, using a uniform scheme of computation, and the discussion of the results obtained in the chapter to follow, will permit us to establish some general hypotheses concerning the relationship between nutrition, growth and metabolism of fish, which must be tested by experiments designed in the light of those hypotheses.

Chapter XII. [page 226]

The Dynamics of the Growth and Metabolism of Fish

1. The significance of the metabolic rate in determining food intake of fish

In order to solve many problems of practical fish rearing it is necessary to know the food rations of various fishes at each stage of their development, and the relation of these to the environment. The accumulation of individual pieces of information in this field, in the form of statements concerning what ration is appropriate to some particular batch of fish under particular conditions, can have practical utility only to the extent that it facilitates the discovery of general laws which make it possible to estimate the rations required under different conditions, or by groups of fish not yet studied. Therefore it is very important to make it possible to distinguish between such relationships among the concrete results of individual studies as suggest basic principles of fish development, and the peculiarities of metabolism which apply only to the experimental animals used or the particular conditions prevailing. How necessary this is can be seen from the material gathered together in G. S. Karzinkin's book, in which are contained the results of many interesting and time-consuming research projects, that have been used for very varied discussions, interpretations and computations. But inasmuch as Karzinkin has not suggested any means to generalize the material accumulated, to distinguish the general from the particular and the characteristic from the incidental, he has failed to indicate how we should use the material he provides in solving practical fish-cultural problems or in obtaining general conclusions of theoretical importance.

The difficulties involved in generalizing diverse and heterogeneous materials do not excuse us from taking the first steps in this direction, steps which will facilitate further searching and indicate to what extent individual investigations might be directed into channels which seem more profitable from the standpoint of both theory and practice.

On the basis of the examples studied above, using the conceptual framework of which the balanced equation is a brief expression (page 210), we will make an attempt [page 227] to study the general relationships of wide applicability among growth rate, food intake, and metabolic rate, which will make it possible to understand the specific peculiarities of individual subjects in future.

In an ideal case, when the calorific equivalent of the body of a fish does not change with growth and remains at 1000 calories per gram of wet weight, 1 mg of oxygen consumed is equivalent to the expenditure of 5 mg of the wet mass of the fish. Hence it is easy to indicate the metabolic rate in the form of relative expenditures of substance or energy for metabolism, expressed as percentages of the weight of the fish. In this situation the moisture content in the body of the fish and its chemical composition are regarded as unchangeable. The magnitudes of the expenditures for metabolism, computed in this way, are applicable equally to the dry weight and the wet, and they also indicate the relative expenditure of energy, or of nitrogen content, in the body of the fish, etc. In reality, as distinct from the ideal situation, the expenditures for metabolism which are computed on the basis of dry weight, wet weight, calorific content, etc., will not agree completely; and they will differ the more, the more the composition of the substances actually used in metabolism differs from the average composition of the body of the fish. However, the relative expenditures for metabolism change so greatly in the course of growth that the general course of these changes can be indicated well enough by the approximate assumptions just made.

It was pointed out above (page 224) that in a majority of cases under natural conditions the mean metabolic rate of fish is about twice as high as the level of routine metabolism. Though these data are not free from discrepancies, in computations of a general nature it is fairly accurate to assume that by doubling the routine metabolic rate we come close to the true mean metabolic rate of fish under natural conditions.

It is important to remember, when studying the interrelations of the processes of growth, food consumed and metabolism, that the values that enter into the balanced equation are not only connected with each other by this equation, but they must also meet another condition. The increase in weight is not only always smaller than the ration, but it also has the definite relationship to the expenditure for metabolism which is indicated by the utilization coefficient. As already indicated (page 196), coefficients of utilization of the physiologically useful part of the food cannot exceed 60-70%, i.e. the expenditures for metabolism cannot be less than 30-40% of the physiologically useful part of the ration, or 37.5-50% of the total ration. Consequently, if the daily ration comprises 50% of the weight, then with maximum possible utilization of food for growth (70%), the expenditure for metabolism will comprise not less than 50 × 37.5 = 18.75%. The metabolic rate cannot increase without limit. There is every reason to believe that for each size of fish there exists a definite, [page 228] maximum possible, average metabolic rate[1]. For this reason a definite limit for the possible ration, and consequently also for growth, must correspond to any given degree of utilization of food for growth. To illustrate this statement, let us assume for the moment that the maximum possible average metabolic rate is twice the value of the routine metabolism, and compute on that basis the maximum possible ration and increase in weight for fish of different weights at various coefficients of utilization of the total food.

Having obtained the expenditures for metabolism from the basic equation, and doubled them, we will base further computations upon the following relationships that arise directly from the determination of the utilization coefficients and the basic balanced equation. We assume, as before, that all values refer to a 24-hour day and are expressed as a percentage of the weight or the energy content in the body of the fish, and that the abovementioned ideal conditions prevail. For brevity we will use the following symbols:

K_1	the coefficient of utilization of the total amount of food,
K_2	the coefficient of utilization of the physiologically useful part of the food,
R	ration (food intake),
P	growth in weight [prirost],
T	expenditures for metabolism [traty].

The basic balanced equation takes the form:

$$0.8\ R = P + T, \qquad (12.1.1)$$

$$K_1 = \frac{P \times 100}{R}; \qquad K_2 = \frac{P \times 100}{0.8\ R} = 1.25\ K_1 \qquad (12.1.2)$$

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[1] The maximum possible average metabolic rate over a prolonged period, which is under discussion here, should not be confused with the maximum metabolic rate during times of active movement.

Hence for any given values of metabolism and utilization coefficients, it is easy to find the corresponding rations and weight increases, which are equal to:

$$R = \frac{T\times100}{0.8(100 - K_2)} = \frac{T\times100}{80 - K_1}, \qquad (12.1.3)$$

$$P = \frac{K_2}{100 - K_2} T = \frac{K_1}{80 - K_1} T \qquad (12.1.4)$$

Thus, with a constant utilization coefficient, growth is directly proportional to the ration (12.1.2), which in turn varies in direct proportion to the metabolic rate (12.1.3 and 12.1.4). Consequently, with a constant utilization coefficient growth and rations are directly proportional.

[page 229] Table 30 contains the approximate maximum values of the metabolic rate of fish of various sizes, expressed as relative expenditures for metabolism per 24-hour day, and the relative values of the corresponding rations and weight gains for 3 different coefficients of energy utilization, computed from formulae (12.1.3) and (12.1.4).

Let us again recall that the values for the rations in the table were obtained by postulating that the chemical composition of the food and of the body of fish do not differ. If, as often happens, the calorific equivalent of the wet weight of the food is smaller than that of the wet weight of the fish, then rations computed on the wet weight basis will be correspondingly larger. For example, if the dry weight content of the food is half as large as that of the body of fish, then the rations when computed as wet weight will be twice as large as those shown in the table.

In contrast to this, the relative gains in weight found for the ideal case can differ only slightly from the corresponding values obtained from actual wet weights, especially if we are considering growth over a short period of time, during which the moisture content in the fish's body cannot change much.

Besides the relationships just formulated, Table 30 also illustrates a number of important relationships between growth rates, rations and gains in weight. For any given value of the metabolic rate (horizontal rows of Table 30), rations increase as the utilization coefficients increase, but not rapidly. When K_2 increases from 5% to 60% the ration increases only to 2.4 times its original level. In contrast to this, the gain in weight depends radically [page 230] upon the degree of utilization of food for growth: when K_2 increases from 5% to 60%, it increases more than 28 times.

In other words, rapid weight increases require not only a high metabolic rate but also a high degree of utilization of food for growth. Even with very high metabolic rates a relatively small drop in the utilization coefficient leads to a sharp decline in the rate of increase in weight.

It is enough to know the metabolic rate and growth rate characteristic of each body size in order to compute the daily ration with sufficient accuracy for all practical purposes. Of course, the result of the computation will reflect the actual rate of food consumption accurately only if the values for weight gain and metabolic rate, on which it is based, are close to the true values.

In many cases the growth rate is accurately enough known. The determination of average metabolic rate of fish under natural conditions is more difficult. This calls for painstaking and difficult research, whose results will, at best, make it possible to obtain only tentative figures for the rations that correspond to the different metabolic rates at the different growth rates.

When computing rations it is most convenient to express the balanced equation in the form:

$$R = 1.25(P + T)$$

Although the general method of computation was explained above, we will give a few examples. It can be seen from Table 30 that at a fish weight of 100 mg, twice the routine metabolism at 20° corresponds to an expenditure for metabolism of 11.3% of the weight. Hence with a daily growth of 5%, which is quite possible for fish of that weight, the ration should be $1.25(5 + 11.3) = 20.2\%$ of the weight of the fish per day. It should be borne in mind that the computation is based on dry weights, and indicates the relation between the wet weight of food and of weight increase only if the moisture content of the fish and of the food is the same. If the food contains 85% moisture and the fish 80%, then in our example the ration on a wet weight basis will be:

$$\frac{20}{15}(20.2) = 26.9\%$$

For fish weighing 100 g, an expenditure for metabolism of 2.9% of the weight per day corresponds to twice the routine metabolism at 20°. Hence for a daily weight increase of 1%, the ration is $1.25(1 + 2.9\%) = 4.9\%$ of the weight of fish per day, when computed on the dry weight of fish and food.

The basic balanced equation can be applied not only to data relating to one day, but it can also be used [page 231] in computing the mean rations for longer periods of time. In this case special attention must be given to the method of obtaining average weight and average metabolism for the period. In situations where growth can be expressed by a straight line during the period studied, the arithmetic mean of the initial and final weight can be accepted as the average weight. In situations where the growth cannot be expressed by a straight line with sufficient accuracy, the average weight must be obtained by a different method, for example, by the simple method of graphical integration. In the same way, if during the period under study the temperature changes greatly, you cannot use the average temperature for the period in computing metabolic rate, since metabolic rate does not increase linearly with temperature. You must find for each temperature the corresponding metabolic rate and get a weighted mean rate from the values obtained. For example, if a fish weighing 100 g was kept 5 days at 20°, 2 days at 18°, 3 days at 23° and then 10 days at 26°, the mean metabolism for the period is computed as follows. According to the basic equation, a metabolic rate of 0.115 ml O_2/g/hour at 20° corresponds to a weight of 120 g. By using Table 1 we obtain the metabolic rate for the remaining temperatures and multiply the values obtained by the number of days of the corresponding period.

20° 0.115 × 5 = 0.575
18° 0.096 × 2 = 0.192
23° 0.131 × 3 = 0.393
26° 0.189 × 10 = 1.891
20 3.051

The weighted mean rate is:

$$\frac{3.051}{20} = 0.152$$

Therefore, in this example 0.152 ml O_2 per gram per hour should be taken as the average routine metabolism for the 20-day period; to which there corresponds, for 80% moisture content, an expenditure for metabolism of 1.82% of the dry weight per day, obtained from formula (11.1.1).

We will now see how the concepts developed above can be applied in computing food rations and overall food coefficients for long periods of time and for fish under natural conditions.

First of all we will transform the basic equation (7.5.3). By multiplying the coefficient (0.3 ml O_2/hour) by 5 we express the general metabolism in calories per hour ($a = 1.5$ cal/hour); also, for a day ($a = 36$ cal/day), and for a month ($a = 1080$ cal/month). The last value is instructive in itself. It indicates that at 20° 1080 cal are spent for the requirements of the routine metabolism of a fish that weighs 1 g, i.e. about as much as is contained in its body. Thus merely to satisfy their energy metabolism requirements for a month at 20°, fish of these sizes must consume a quantity of food of high calorific content that somewhat exceeds their body weight. If the calorific content of the food is less than that of the fish, let us say half the latter, then the weight of the food consumed must be doubled.

By continuing these obvious transformations of the basic equation we find that, taking a year as the unit of time, $a = 13140$ cal (at 20°). Only rarely could this last value be used directly, because in countries with a temperate climate thermal conditions change radically in the course of a year, and these must be considered when computing the food requirements of fish.

We will use data from the very interesting and important work of M. G. Dadikīan (1955) to illustrate the computations with concrete material. Dadikīan, on the basis of careful quantitative investigations of the feeding of the different races of Lake Sevan trout, computed the yearly rations and food coefficients for each age of each of the four races. In this thorough work he presents the sizes of the age-groups and the temperature conditions in Lake Sevan. This makes it possible, using the concepts developed here, to compute the expected size of the rations and the food coefficients, and to compare them with the values of the same parameters obtained by quite different and unrelated methods by Dadikīan.

From the information in the text, and from supplementary data kindly provided by the author, it can be taken that the average monthly temperatures in places the trout prefer (bearing in mind their migrations) are close to those indicated in Table 31.

[page 233] The last row in the Table shows the coefficients obtained from Table 1; using them as divisors, the computed values of metabolism can be reduced to the required temperatures. The expenditures for metabolism for each month separately could be obtained, but since it can be assumed that the months are of the same length, it is reasonable to use the shortest form of computation, which in this instance is fully applicable. After adding all the coefficients and dividing the sum by 12 we get their mean value, 3.37, which can be used to transform expected values for metabolism to the temperatures that prevail in Lake Sevan. Hence for the actual conditions:

$$a = \frac{13140 \text{ cal/year}}{3.37} = 3900 \text{ cal/year}$$

Consequently, the basic equation takes the form below for the Lake Sevan trout:

$$Q \text{ (cal/year)} = 3900w^{0.8} \qquad (12.1.1)$$

If we take twice the value of the routine metabolism, then:

$$Q\ (\text{cal/year}) = 7800w^{0.8} \qquad (12.1.2)$$

Now, using figures given in table 40 of the article by Dadikian for the mean weights and annual gains in weight of different weight-groups of trout that belong to the fast-growing race--the gegarkuni, and to the "dwarf" race--the bodzhak, it is easy to compute the expected sizes of the rations and food coefficients.

To illustrate this we give a computation for age-group 4+ of the gegarkuni. The mean weight of fish of this age is 298 g. Hence from formula (12.1.1) we find that the expenditures for metabolism for a year are 372,000 cal. According to Dadikian's data the annual increase in weight is 124 g, which for trout must be close to 124,000 cal. Hence the sum of the expenditures for metabolism and weight increase amounts to 496,000 cal. We multiply this sum by 1.25, which amounts to 620,000 cal, in order to obtain the annual ration. By dividing this last figure by the annual weight increase, expressed in calories, we find that the food coefficient on a calorific basis amounts to 5.00. In order to convert to a food coefficient on a weight basis so as to compare them with the values obtained by Dadikian, we must know the mean calorific equivalent of the food organisms upon which trout feed. Bearing in mind that amphipods comprise 86-96% of the ration of Sevan trout, we can take the mean calorific value of the food of Sevan trout as 675 cal. In this case the values obtained for the food coefficient must be increased by $\frac{1000}{675} = 1.48$ times. From this: $5 \times 1.48 = 7.4$.

[page 234] If, in the computation, twice the value of the routine metabolism is used as a starting point, we obtain from the same initial data and formula (12.1.2) that the annual ration of an age 4+ gegarkuni amounts to 1,083,000 cal, while the food coefficient on a calorific basis is 8.73, and on a weight basis is 14.7. Dadikian obtains a food coefficient of 13.7 for this age-group.

For the other age-groups the computed food coefficients and those observed by Dadikian are shown in Table 32. Two figures are shown for the computed values for annual rations and food coefficients, in columns 5 and 6. The first was obtained by assuming that the mean metabolic rate of trout under natural conditions is equal to the "routine" metabolism; the second figure assumes that this rate is twice as high.

The first figures are minimal. They are obviously lower than the true values, which latter most likely approach the second figures. It is a matter of interest that for the older age-groups of the slow-growing race even the minimal values of the food coefficient are rather large.

It is noteworthy that a computation made independently of the data on feeding has led to values for the food coefficient which in general are similar to those found by Dadikîan (last column, table 32), and reflect the peculiarities of the two races very well. But there is also an important difference. Dadikîan gives much higher food coefficients for the older ages.

The question arises, which come closer to the true food coefficients--the results from our tentative [page 235] computations or the figures obtained by Dadikîan, based on a laborious and meticulous study of the feeding of trout in Lake Sevan, over a long period of time? I need only mention that he examined the contents of 3454 stomachs by quantitative methods! There is reason to think that Dadikîan obtained overestimates of the food coefficients, especially for the older age-groups. The fact is that, in spite of his large and useful body of material, in making his calculations he was compelled to make use of a number of more or less arbitrary assumptions. For example, he assumed that the number of times the alimentary tract was filled per day was the same for fish of all ages, which can scarcely be true. It is possible that it is partly a result of this assumption that according to his calculations the rations per unit weight do not change with age, something which is extremely unlikely: for as the size of a fish increases, both its expenditures for metabolism and its relative growth rate decrease.

An argument already published, favouring the view that Dadikîan arrived at extremely high food coefficients, is the fact that from his data he computed that the trout in Lake Sevan consume annually 7992 tons of amphipods, which is twice the annual production of amphipods in the lake as computed by A. K. Markosîan on the basis of his special study.

On the whole, it cannot be denied that very encouraging results have come from the comparison of the food requirements of the Sevan trouts (calculated from the expected metabolic rate) with the data from Dadikîan's painstaking and protracted study of the food of these fish. These indicate that the method used is suitable, and point to the need for its further perfection and development.

Similarly, using the basic equation to obtain expected values for metabolism, formula (11.1.1) to convert the metabolic rate to the form of expenditures for metabolism per day, and Table 1 to make the necessary corrections for temperature, it is easy to compute approximate figures for the ration of fish of any weight, at whatever temperature is necessary. Naturally the computation will always represent the actual size of the ration the more accurately, the more accurately determined are the temperature to which the computation refers, the metabolic rate, the growth rate, and also the digestibility of the food, which in some cases will differ from the figure 1.25 used in these tentative computations. Given accurate information, for particular fish and particular conditions, on the metabolic rate, digestibility of the food, calorific content of the fish and the food, the moisture content of the fish, etc., it is possible [page 236] to increase the accuracy of the computations to any desired degree. But the basis of the computations, which has been illustrated by these approximate examples, remains unchanged.

2. Types of dynamics of growth and nutrition of fish

The interrelationships of the processes of growth and metabolism of growing fish is to be pictured in the following way. During the initial period of post-embryonic growth food is used very effectively for growth; the coefficients of food utilization have high values, for example 50-60% for K_1. These high values of the utilization coefficients are maintained for some time at the same level, or else they decrease so slowly that they can be considered as almost uniform over this period. Of course, constancy of the coefficients of utilization is not to be interpreted in the sense of absence of variations caused by changes in feeding conditions, which can be quite large, but only in the sense of a relative constancy under unchanging conditions--for example, optimum conditions. To me it seems that maintaining this steady and high level of the coefficient of utilization of food for growth is the most characteristic feature of the first period of growth of the young fish; the other characteristics can be regarded as results of this circumstance and of the decrease in metabolic rate with increase in size. As explained above, with a constant coefficient of utilization the maximum ration and growth change in direct proportion to the metabolic rate, i.e. with increasing size they fall off at the same rate as the metabolic rate does.

Starting at some particular stage of development, a decline in the effectiveness of the utilization of food for growth is observed, so that the maximum value of the ration, and consequently growth also, are reduced proportionally. Now that the coefficients of utilization of food for growth no longer remain constant, the reduction of the ration with increase in size does not run parallel to the reduction in metabolic rate, as was true during the first period of growth, but it becomes more rapid. The amount of daily growth, which as shown above (page 229) depends greatly upon the coefficient of food utilization, falls off even more rapidly. At this time there takes place a rather rapid transition from the initial period of rapid growth to the next period, in which growth of the fish proceeds at a considerably slower pace.

When growth rate is slow, size increases little during any rather short period of time. Correspondingly, the metabolic rate also is only slightly reduced. Under these conditions the metabolic rate can, without stretching matters, [page 237] be regarded as constant over short intervals. With a constant metabolic rate, the direct relationship between growth and food intake stands out prominently; under these conditions the ration can be derived directly from the balanced equation. Whereas during the first period of growth 50% or more of the food consumed was utilized for growth, now that the daily growth is only 1-2% or a fraction of a percent [of the body weight], a correspondingly small fraction of the food is used for growth, and the size of the ration is determined mainly by the metabolic rate.

The outline just presented, of changes that accompany the growth of a fish, has general significance and can be applied equally to any species of fish. The question arises of to what extent the observed phenomena differ between different species of fish, within this scheme. It should be observed that the indices which represent the rates of the processes of growth, feeding, and metabolism, taken by themselves, cannot indicate the individual peculiarities of each species. For one thing, the rates of the vital processes are greatly dependent upon temperature and other environmental conditions. However, even if the growth of fish is studied under conditions that are optimal for each species, the magnitudes of the rates of these processes, taken by themselves, still tell nothing about individual peculiarities of the species. Any fish at all, at some particular moment in its development, will have a daily weight increase of 5%, let us say, or a metabolic rate of 0.3 ml O_2 per g of weight per hour, and so on. The parameters of these processes can serve this purpose [indicate species differences] only if we also know the age, size, weight or other appropriate quantities which directly or indirectly indicate to what stage of growth the given parameter of a vital process applies to. Consequently, in these cases we are actually studying the relation between the rate of a given process and its total result as expressed in some form or other at a certain stage of development. It would seem that this should not require explanation. However, the differences brought to light by experiment, between rates of various processes, are quite often facilely ascribed to the "specificity" of the subjects studied (Karzinkin, 1952).

For example, G. S. Karzinkin compares the daily ration of mature verkhovka with the daily ration of the marine scorpionfish, the zander, mature pike, and pike weighing 1026 g. Though Karzinkin considered it unnecessary to mention the size or weight of the scorpionfish or zander, we may assume that mature specimens were involved. Stating that the daily ration of verkhovka is considerably higher than that of the other fish used, Karzinkin ascribes this directly to the plankton-

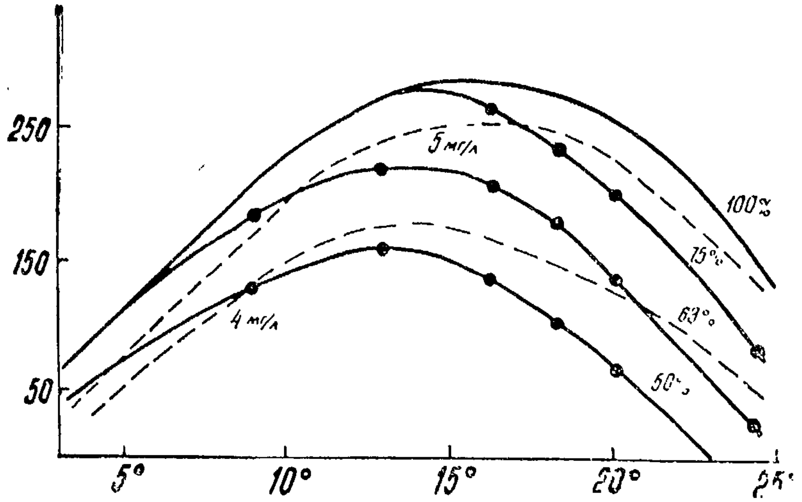

Fig. 54 [page 179]

Difference between maximum active metabolism and resting metabolism of the American char [brook trout] at various temperatures and environmental oxygen contents. The solid curves correspond to the indicated magnitudes of percentage oxygen saturation of the water; the dotted curves show the oxygen content in mg/l.

Abscissa--temperature; ordinate--difference between the oxygen consumption rates, in ml/kg/hou (Graham, 1949).

eating habit of verkhovka, and writes that "the higher [food] consumption of plankton eaters is particularly marked, in comparison with the feeding of mature predators" (page 228). This conclusion can scarcely be regarded as convincing, for it is derived by comparing the rations of verkhovka weighing about [page 238] 1.5 g with the rations of fish which weighed hundreds of grams, or even kilograms! As we discovered earlier (page 105, Table 8, page 219), the metabolic rate of the verkhovka does not differ much from corresponding figures for other fish of the same size. As for rations, for verkhovka these are, characteristically, not larger but smaller than the rations of the other fishes studied, i.e. fish of a similar weight (Table 26). In order to establish a possible relationship between the ration and type of feeding (plankton-feeder or predator) one should at the least compare fish of the same weight. Furthermore, it must not be assumed that all plankton feeders, for example the ripus which attains a weight of 1 kg, or the blue bream which often is even heavier, have the same relative rations when mature as do verkhovka weighing 1.5 g. It is easy to see that this is simply impossible; for one would have to assume that the metabolic rate of such large fish is the same as the metabolic rate of the verkhovka. Actually, of course, it is several times less. Therefore there is no reason to assume that mature plankton feeders have higher rations than predacious fishes of the same weight. Of course, in studying this question as a whole it might prove that rapid maturity, and the small size of mature specimens, is one of the ways in which plankton feeders are adapted to the conditions of their way of life, but that is a different matter. In that event, for plankton feeders whose adaptation to their environment has taken this direction, it will actually be possible to establish a characteristic type of development associated with the limited efficiency of the utilization of food by these fish. Obviously the efficiency of utilization of food by such small species will be less than in the case of large predators or large plankton feeders. Similar differences may be established between large predators and small predators, etc. One of the manifestations of adaptation to feeding upon small organisms (plankton) may be such a type of growth, and such relationships between growth and metabolism, as will be adequate at low rations. For example, this might be achieved by an early decrease of rate of growth during development.

I believe that during the first period of growth of fish when, with high efficiency of utilization of food for growth, the size of the ration and consequent rate of increase in weight are mainly determined by the maximum possible metabolic rate, species differences in the processes of growth and metabolism are relatively weakly developed, just as during this initial period there is little evidence of biological differences either--for example, in qualitative composition of the food or in mode of life. During the early stages of growth species differences take the form, primarily, of how long the capacity for a high level of food utilization for growth can be maintained; or, more correctly, up to what [page 239] size growth can continue at a high coefficient of utilization. Among rapidly maturing fish with small definitive size the food utilization coefficients cannot remain at a high level for any very long time. For such fish as verkhovka the daily weight increase and rations become very small at a size which, in fish like pond carp or wild carp, the capacity for rapid growth and high food utilization coefficients are still fully retained. In this connection it must be remembered that the metabolic rate of the verkhovka is apparently close to or the same as that of carp of the same weight (Fig. 30).

Although it is difficult to attach special significance to one of the aspects of the course of development characteristic of a species, separating it from its historically associated system of processes, it is nevertheless possible to consider the matter of what, primarily, is associated with the decline in effectiveness of utilization of food for growth--a decline which occurs at a moment in development which is different for different species. For any definite type of adaptation to the environment inherent in a species, or specifically when there is a congenitally-determined type of feeding and behaviour that begins at a certain moment in its development, then the morphological and physiological peculiarities and the behaviour of the fish begin to limit the rate of food intake (the ration), with the inevitable result that the utilization coefficients and growth become less. We might imagine that low rations become established as a result of earlier differentiation, in the case of early-maturing fish of small size, which excludes the possibility of growing rapidly, since high rations have become unnecessary and impossible. In addition, we might postulate that in some species of fish, starting at a certain size, a relatively large part of the total metabolism is spent in movement; this, however, has yet to be demonstrated.

In contrast to rapidly maturing fish, in carp and especially in sturgeon the capacity for growth with effective utilization of food is long retained (Table 28). With these fish the ration and the growth rate remain at a relatively high level even when their weight and size are considerable, which makes it possible for them to grow to a large size.

By means of the above examples I have tried only to emphasize that the food ration at different stages of development, and for different species of fish, constitutes one of the quantitative characteristics of the metabolism of a growing organism, which cannot be understood without knowing the quantitative interrelations of the processes of growth and metabolism. Species differences in respect to rations, and other indices of the individual aspects of metabolism and growth, can be formulated accurately only if the type of development inherent in the organism in question is taken into consideration, when it is known at what stage of its increase in size [page 240] the change takes place in the relationship between the processes of utilization of food for growth and its expenditure for metabolism.

Only if these quantitative relationships between the separate aspects of a growing organism are known, or when there is at least a definite method for describing them, can we proceed further and study the problem of what ecological features the inherent physiological type of development of a given species corresponds to. Otherwise, when an attempt is made to compare directly such factors as the species composition or size of food organisms with the quantitative measure of any aspect of metabolism (such as, for example, the daily ration), the door will be opened wide to unreliable, arbitrary and erroneous conclusions.

In comparing the results of two experiments in which young pike were fed with Daphnia and roach fry, Karzinkin comes to the conclusion that the "influence of the size of the food organism on the magnitude of the food coefficient is quite clear" (page 243). Actually, as can be seen from the last lines of his tables 42 and 71, the whole effect observed consists in the fact that when the pike used in the experiments were fed on Daphnia they ingested considerably less food[1] during the final periods of the experiment and consequently they grew at a slower pace. Under these conditions the food coefficient must inevitably be higher. In other words, it is simply that, beginning at a certain size, the young pike can no longer meet their food requirements by feeding on Daphnia.

In other words, the experiment reveals not the physiological but the biological inferiority of Daphnia as food for young pike, in the sense that the larger pike fingerlings cannot consume them in sufficient quantity. This is what should be stressed, and not the "effect on the magnitude of the food coefficients", i.e. the extent to which the food is used for growth. The [percentage] utilization of Daphnia for growth would not have differed substantially from the utilization of young fish, if the Daphnia could have been consumed by the growing pike in sufficient quantity. Karzinkin of course is well aware of this; in another place in his book he writes: "A very mobile, hence less accessible, food such as Diaptomus, if the inaccessibility factor is eliminated by increasing the food offered, shows a percentage utilization of nitrogen for growth which is even somewhat better than that obtained from moth larvae" (page 259). This means that biological inequality

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[1] Remember that for equal wet weight the calorific content of Daphnia is considerably less than that of young fish.

of foods, in contrast to physiological inequality, affects the processes of growth and metabolism not by way of a difference in effectiveness of utilization for growth, but only by way [page 241] of differences in consumption. In the establishment of these relationships in the process of adaptative evolution, the biological inequality of foods and, in general, the nature of the trophic and other ecological relationships characteristic of a given species, are reflected in the type of dynamics of growth and metabolism during development that is peculiar to it. For example, after a certain size is reached, feeding on zooplankton can be associated with a slow rate of growth, and so on.

* * *

The examples considered show how necessary it is, when conducting quantitative research on the food rations of fish, and their utilization of food for growth, to go beyond the purely empirical accumulation of individual items of information obtained from different subjects by different methods; and how necessary it is to have a system of concepts, even if it be incomplete, which can provide a means of generalizing the motley and heterogeneous empirical material, and can to a certain extent direct individual research projects and enhance their effectiveness. The basic purpose of this attempt to provide a general method of expressing quantitatively the relationships between fish metabolic rates, food rations and growth, is to meet this acute need.

The concepts that have been formulated regarding the metabolic rate and food requirements of fish, the generalizations made from actual material, the methods suggested for the calculations, and the alternative objectives for research that have been outlined, must all be defined and suited to each separate subject of physiological, ecological and fish-cultural research. By indicating several means of establishing general quantitative laws of fish metabolism I have hoped to further the development of knowledge in the fields of physiology and ecology of fish in a direction directly related to the solution of a number of urgent practical problems of fish culture and management in the USSR.

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[Common abbreviations used below include:

AN SSSR--Akademii͡a Nauk SSSR

AN UkrSSR--Akademii͡a Nauk Ukrainskoĭ SSR

BGU--Belorusskiĭ Gosudarstvennyĭ Universitet

MGU--Moskovskiĭ Gosudarstvennyĭ Universitet

MOIP--Moskovskoe Obshchestvo Ispytateleĭ Prirody

Mosrybvtuz--Moskovskiĭ Tekhnicheskiĭ Institut Rybnoĭ Promyshlennosti i Khozi͡aĭstva

VNIORKh--Vsesoi͡uznyĭ Nauchno-Issledovatelskiĭ Institut Ozërnovo i Rechnovo Rybnovo Khozi͡aĭstva

VNIRO--Vsesoi͡uznyĭ N.-I. Institut Morskovo Rybnovo Khozi͡aĭstva i Okeanografii

TINRO--Tikhookeanskiĭ N.-I. Institut Rybnovo Khozi͡aĭstva i Okeanografii]

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[1] This list of references is in no way an exhaustive review of the literature on the rate of metabolism of fishes; it consists mainly of the works which have been referred to in the text. Nevertheless it probably includes all the more important studies containing quantitative data on fish metabolic rates which saw the light prior to 1954, and some, particularly Soviet works, which were published during 1954.

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Table 1. [page 33] Table of factors (q) for adjusting values of metabolism to 20°, on the basis of the "normal curve".

T°	q	T°	q	T°	q	T°	q	T°	q
5	5.19	10	2.67	15	1.57	20	1.00	25	0.659
6	4.55	11	2.40	16	1.43	21	0.920	26	0.609
7	3.98	12	2.16	17	1.31	22	0.847	27	0.563
8	3.48	13	1.94	18	1.20	23	0.779	28	0.520
9	3.05	14	1.74	19	1.09	24	0.717	29	0.481
								30	0.444

$$q = Q_{10}^{\frac{20-T}{10}}$$

Table 2. [page 64] Environmental oxygen content (mg/l) at which inhibition of respiration begins, and that at which death ensues, at temperatures close to 0° (according to Privolnev, 1954).

Name of fish	Beginning of inhibition of respiration	Time death sets in
Sterlet	7 - 7.5	3.5
Inconnu (nelma)	6 - 7	4.0 - 4.5
Muksun	4 - 4.5	1.5 - 2.0
Peli͡ad	3.5 - 4.0	1.0 - 1.5
Ladoga whitefish	-	1.6 - 5.2
Brook trout	-	1.1 - 3.3
Rainbow trout	-	0.8 - 1.2
Ural ripus	-	0.95
Burbot	-	1.4 - 3.2
Bream	2.0 - 2.5	0.4 - 0.5
Zander	1.5 - 2.0	0.5 - 0.8
Perch	2.0 - 3.0	0.2 - 0.6
Ide	3 - 4	0.5
Roach	2 - 3	0.7
Pike	2 - 3	0.3 - 0.6
Pond carp	1.5 - 2	0.2 - 0.3
Tench	1 - 2	0.1 - 0.2
Crucian carp	1 - 2	0.1

Table 3. [page 97] Composite table of measurements of rate of oxygen consumption of goldfish.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Carassius auratus	Baudin 1931	I	C	20	6.2 ml/fish/hr	72	0.086
2	" "	" "	I	1	10	4.1 " "	100	0.109
3	" "	Baudin 1931a	I	C	9	4.0 " "	100	0.122
4	" "	" "	I	60[1]	12-18	2.7-5.0 " "	32.5	0.150
5	" "	Baudin 1932	I	4	15	2.54 " "	33	0.120
6	" "	Ege & Krogh 1914	I	C	20.1	1.83 ml/kg/min	9.3	0.110
7	" "	Fry & Hart 1948	I	C	20	85 ml/kg/hr[2]	3.8	0.085
8	" "	Gardner 1926	II	C	21	80 " "	51	0.074
9	" "	Hasler 1942	III	35	20	0.190 mg/g/hr	29	0.133
10	" "	Jolyet and Regnard 1877	II	2	12	45.7 ml/kg/hr	36.4	0.098
11	" "	" " "	II	1	12	29.9 " "	111.2	0.064
12	" "	Raffy 1931	I	9	19	0.151 ml/g/hr	2.45	0.170
13	" "	" "	I	3	19	0.149 " "	1.57	0.162
14	" "	Raffy 1933	I	4	20	0.195 " "	9.5	0.195
15	" "	Raffy 1932	I	2	20	0.114 " "	4.95	0.114
16	" "	Spoor 1946	III	C	24	0.075 ml/g/hr[3]	32	0.054
17	" "	Toryu 1928	I	C	19	0.101 " "	21	0.110
18	" "	Rubner 1924	—[4]	4	16.6	12.77 cal/kg/day	3.9	0.143
18a	" "	" "	—[4]	4	20.8	20.63 " "	3.9	0.148
19	" "	Bounhiol 1905	II	1	18.5	0.039 ml/g/hr	130	0.045
20	" "	" "	II	1	18.5	0.036 " "	82.5	0.041
21	" "	" "	II	1	18.5	0.041 " "	39.5	0.046
22	" "	Putter 1909	I	C	16	0.582 mg/fish/hr	5.94	0.098

[1] Average for 6 series of observations.

[2] 20 fish in the respirometer. Lowest metabolism observed during 24 hours.

[3] Basal metabolism (metabolism during minimum activity).

[4] Direct calorimetry.

Table 4. [page 101] Composite table of measurements of rate of oxygen consumption of carp.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at 20°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Carp	Knauthe, from Cronheim 1927	II	C	20	2200 ml/kg/day	602	0.092
2	"	" "	II^1	3	17.4^1	27.7 cal/kg/day	12.2	0.316
3	"	" "	II	15	17.0^1	11.4 " "	241	0.124
4	"	" "	II	22	17.5^1	8.7 " "	573	0.091
5	"	" "	II	1	20.8^1	7.94 " "	1217	0.062
6	"	Knauthe 1898	II	3	19.0	3734 ml/kg/day	793	0.170
7	"	" "	II	2	20.6	3663 " "	335	0.145
8	"	Khalil 1937	III	10	11	0.0303 ml/g/hour	345	0.072
9	"	Oya & Kimata 1938	III	C	19	~0.090 ml/fish/min^2	20.9	0.281
10	"	" "	III	C	19	~0.070 " "	17.4	0.270
11	"	" "	III	C	19	~0.045 " "	10.4	0.283
12	"	Adrianov 1937	I	7	19.5	0.113 ml/g/hour	113	0.118
13	"	Streltsova 1953	I	5	10.5	85.0 ml/kg/hour	25.6	0.216
14	"	" "	I	9	9.8	150.0 mg/kg/hour	24.7	0.289
15	Scaly carp	" "	I	4	9.5	53.1 ml/kg/hour	331	0.152
16	Mirror carp	" "	I	4	8.25	39.6 " "	320	0.134
17	" "	Ivlev 1954	III	1	19	10.08 mg/fish/hr	39.8	0.194
18	" "	" "	III	1	19	370.5 " "	2831	0.100
19	" "	" "	III	1	19	611.1 " "	3487	0.133
20	" "	Ivlev 1938	III	C	20	~ 43 mg/kg/hour	35	0.030^3
21	" "	Stroganov 1949	I & III	C	14	~ 90 ml/kg/hour	74	0.157^4
22	" "	Briukhatova 1939	I	9	19	0.24 ml/g/hour	9	0.261^5
23	" "	" "	I	9	19	0.19 " "	9	0.207
24	" "	Novikova 1939	III	2	17	0.255 mg/g/hr	17.5	0.235

Table 4 (continued)

25	Mirror carp	Mints 1952	I	5	16.5	0.25 mg/g/hour	8.7	0.247
26	" "	Privolnev 1947	I	3	20	283 mg/kg/hour	39	0.198
27	" "	" "	I	2	20	363 " "	12.5	0.254
28	" "	" "	I	19	20	400 " "	2.5	0.280
29	" "	Schmeing-Engberding 1953	III	C	20	1.285 ml/fish/hr	4.35	0.295
30	Carp	Krivobok 1953	I	1	20.6	0.110 mg/fish/day	0.0032	0.948[6]
31	"	" "	I	1	21.9	0.492 " "	0.0263	0.465
32	"	" "	I	1	25.5	3.339 " "	0.140	0.487
33	"	" "	I	3	25.1	36.14 " "	2.69	0.240
34	"	" "	I	1	24.0	11.53 " "	0.560	0.373
35	"	" "	I	1	29.9	15.81 " "	0.700	0.290
36	"	" "	I	1	30.4	35.91 " "	1.510	0.291

[1] From data of Table 4 at $Q_{10} = 2.45$.

[2] Read from figures.

[3] Measured in winter, using fish "in poor condition", page 656.

[4] Measured in winter.

[5] Kept in an aquarium.

[6] Beyond the limits of the graph of Fig. 29.

Table 5. [pages 108–109] Composite table of measurements of rate of oxygen consumption of acipenseroid fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Osëtr (fry)	Korzhuev 1941	M[1]	C	20	~6 mm^3/mg dry wt./hr	0.023	0.900[1]
2	" "	" "	M	C	20	~2.5–3 " "	0.467	0.412
3	Sevriuga	" "	M	C	20	~6 " "	0.023	0.900
4	"	" "	M	C	20	~3 " "	0.433	0.450
5	Sevriuga (fry[2])	Lozinov 1950[10]	III	C	18	522 mg/kg/hour	0.225	0.418
6	" "	" "	III	C	25	847 " "		
7	Sevriuga fingerlings	" "	III	C	18	452 " "	6.12	0.353
8	" "	" "	III	C	25	727 " "		
9	Osëtr (fry)	" "	III	C	18	359 " "	0.3	0.290
10	" "	" "	III	C	25	605 " "		
11	Osëtr fingerlings	" "	III	C	18	272 " "	12.5	0.235
12	" "	" "	III	C	25	526 " "		
13	Sevriuga	Streltsova 1953	I	15	20	68.2 "	6500	0.068
14	Sterlet	" "	I	6	20.7	152 " "	205[3]	0.143
15	Osëtr	" "	I	1	18	69.6 "	208	0.083
16	"	" "	I	3	21	176 " "	54.3	0.162
17	Ship	" "	I	4	19	136 " "	89	0.148
18	Sevriuga	Olifan 1945	I	C	21	0.7 ml/g/hour	0.033	0.644
19	"	" "	I	C	21	0.375 " "	0.800	0.345
20	Sterlet	Privolnev 1947	I	C	10	~70 mg/kg/hr	287	0.131
21	Sterlet[4]	Svirenko 1948	III	C	20	34.9 mg/kg/hour	258	0.135
22	Sevriuga[5]	" "	III	3	24.4	244.3 " "	3700	0.119
23	Sevriuga[6]	" "	III	15	21.8	170.8 " "	6050	0.103
24	Sevriuga[7]	" "	III	19	22.4	148.2 " "	7520	0.085
25	Sevriuga[8]	" "	III	6	22.5	104.7 " "	10400	0.059

Table 5 (continued)

26	Sevriuga fry	Svirenko 1948	I	160	21.1	1037 mg/kg/hour	0.045	0.640
27	" "	" "	I	64	21.7	1047 " "	0.063	0.638
28	" "	" "	I	51	22.1	1035 " "	0.086	0.608
29	" "	" "	I	C	20.5	1040 " "	0.164	0.699
30	" "	" "	I	C	17	548 " "	0.65	0.502
31	" "	" "	I	C	17	320 " "	1.75	0.293
32	Hybrid: osëtr × sevriuga	" "	I	2	22.7	817 " "	4.95	0.457
33	" "	" "	I	3	23.1	374 " "	16.0	0.202
34	Sevriuga (young)	" "	I	2	23.0	1110 " "	3.74	0.605
35	" "	" "	I	1	22	705 " "	10.42	0.418
36	" "	" "	I	C	20	531 " "	3.62	0.372
37	Sterlet	Stroganov 1949	III	7	6.5	57.14 ml/kg/hour	304	0.078

[1] Calculated assuming 85% moisture.

[2] Average for the age of 39-53 days.

[3] Extremes of weight were 51 and 800; no relation of metabolism to size could be detected.

[4] Average data for sterlets No. 5-No. 8, measured at 18-25°. Large number of measurements.

[5] 1 fish.

[6] 4 fish.

[7] 5 fish.

[8] 5 fish.

[9] On Fig. 31 the data of No. 1 and No. 3 coincide, as do 2 and 4; they are shown by two points.

[10] In Tables 5, 7 and 11, Lozinov's data are from his dissertation of 1950.

Table 6. [pages 110-111] Composite table of measurements of rate of oxygen consumption of salmonoid fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Trout	Gardner 1926	II	C	20	196 ml/kg/hour	23	0.196
2	"	" "	II	C	20	210 " "	96.4	0.210
3	*Salvelinus fontinalis*	Graham 1949	III	C	20	140 " "	23.2	0.140[5]
4	*Salmo salar*, age 36 days	Lindroth 1942	I		15	0.04 ml/fish/hr	0.15	0.420
5	" " age 3 years	" "	I	C	20	2.9 " "	16	0.180
6	" " age 4 years	" "	I	C	20	4.0 " "	25	0.160
7	Rainbow trout	van Dam 1938[1]	I	?	19	107 " "	900	0.119
8	*Plecoglossus altivelis*	Oya and Kimata 1938	III	C	19	~0.10 ml/fish/min[2]	10.7	0.600
9	*Salmo fario*	Raffy 1933	I	7	20	0.354 ml/g/hour	2.15	0.354
10	*Salmo fario*[3]	Washbourn 1936	I	10	10	116 ± 4.5 ml/kg/hr	0.671	0.310
11	*Salmo fario*[4]	" "	I	10	10	91 ± 7 " "	0.583	0.243
12	Neva smelt	Streltsova 1953	I	6	14.7	157.5 ml/kg/hour	38.3	0.254
13	Ladoga whitefish	" "	I	3	12.3	132.3 " "	210	0.277
14	Muksun	Privolnev 1948	I	2	10	32.2 mg/kg/hour	1892	0.060
15	"	" "	I	1	20	39.0 " "	1710	0.027
16	*Stenodus leucichthys nelma*	Privolnev 1947	I	C	10	~70 " "	192.5	0.131
17	Inconnu (fry)	Svirenko 1948	I	C	9.75	1136 mg/kg/hour	0.01	2.18
18	" "	" "	I	C	21.2	930 " "	0.97	0.785
19	" "	" "	I	C	21.2	776 " "	1.72	0.488
20	" "	" "	I	C	21.2	629 " "	2.51	0.396
21	Rainbow trout	Lindstedt 1914	II	3	14	211.6 ml/kg/hr	202	0.367[6]
22	Salmon (young)	Privolnev 1953	I	?	15	480 mg/kg/hr	1.5	0.527
23	" "	" "	I	?	15	305 " "	5	0.336

Table 6 (continued)

24	Salmon (young)	Privolnev 1953	I	?	15	250 mg/kg/hour	10	0.274
25	" "	" "	I	?	15	210 " "	20	0.230
26	" "	" "	I	12	15	400 " "	5	0.440
27	" "	Nikiforov 1953	I	3	14.5	750 " "	0.17	0.865
28	" "	" "	I	3	14.5	520 " "	2.5	0.600
29	" "	" "	I	3	14.5	252 " "	10.0	0.291
30	<u>Trutta iridea</u>	Halsband 1953	III	2	15	2.55 ml/fish/hr	14.3	0.280

[1] According to Lindroth (1942).

[2] 24-hour mean, from Fig. 3.

[3] Narcotized, slow current.

[4] Narcotized, swift current.

[5] Minimum metabolism observed in a 24-hour period.

[6] Moved actively. 2-4 fish used in the experiment.

Table 7. [page 115] Composite table of measurements of rate of oxygen consumption of tench.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	*Tinca vulgaris*	Hee & Bonnet 1925	I	35	13	6.32 ml/fish/hr	150	0.082
2	*Cyprinus tinca*	Jolyet and Regnard 1877	II	1	14	55.7 ml/kg/hour	222.5	0.097
3	*Tinca vulgaris*	Khalil 1937	III	12	11	0.0193 ml/g/hr	190	0.046
4	Tench	Raffy 1932	I	1	20	6.355 ml/fish/hr	41	0.155
5	"	" "	I	1	20	3.490 " "	18.5	0.189
6	*Tinca tinca*	Ivanova 1939	I	1	18	0.155 mg/g/hour	5.85	0.130
7	" "	" "	I	1	18	0.138 " "	7.0	0.116
8	Tench	Lozinov 1950			18	96 mg/kg/hour	30.5	0.081
9	*Tinca tinca*	Bounhiol 1905		1	18.5?	0.0557 ml/g/hr	222.5	0.064
10	Tench, 3-year-olds[1]	Lindstedt 1914	II	7	13.4	46 ml/kg/hour	226	0.085
11	" "[1]	" "	II	5	22.1	78.5 " "	187	0.066
12	Tench, 2-year-olds[2]	" "	II	5	16.1	76.6 " "	32.4	0.108
13	" "[3]	" "	II	4	17.1	105.2 " "	32.7	0.132
14	Tench fingerlings[2]	" "	II	3	17.05	108.7 " "	8.4	0.142
15	" "[3]	" "	II	1	17.0	159.0 " "	8.1	0.208
16	" "	Mints 1952	I	5	16.0	0.20 mg/g/hour	1.35	0.200
17	Tench, 2-year-olds	" "	I	5	15.0	0.10 " "	118.9	0.110

[1] Not fed; lost weight.

[2] Not fed.

[3] Fed.

Table 8. [pages 116-117] Composite table of measurements of rate of oxygen consumption of freshwater cypriniform fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	*Cyp. phoxinus*	Jolyet & Regnard 1877	II	1	16	140.0 ml/kg/hr	4.84	0.200
2	*Cobitis fossilis*	" "	II	1	19.5	86.3 " "	15.83	0.086
3	*Idus melanotus*	Khalil 1937	III	9	11	0.0266 ml/g/hr	276	0.064
4	Rudd	Szarca 1930	III	8	20	5.2 g/kg/day	53	0.152
5	*Misgurnus fossilis*	Ivanova 1939	I	1	18	0.123 mg/g/hr	28.5	0.103
6	*Cobitis taenia* L.	" "	I	2	18	0.171 "	4.2	0.144
7	*Nemachilus barbatulus*	" "	I	1	18	0.235 "	12.2	0.197
8	" "	" "	I	1	18	0.275 "	4.4	0.231
9	*Leucissus cephalus*	" "	I	1	18	0.282 "	3.04	0.237
10	" "	" "	I	1	18	0.267 "	12.9	0.224
11	" "	" "	I	3	18	0.180 "	168	0.151
12	*Abramis brama*	" "	I	1	18	0.135 "	102.9	0.114
13	" "	" "	I	1	18	0.196 "	69.5	0.165
14	" "	" "	I	1	18	0.210 "	38.7	0.177
15	*Gobio gobio*	" "	I	1	18	0.350 "	1.2	0.294
16	" "	" "	I	1	18	0.331 "	3.87	0.278
17	" "	" "	I	1	18	~0.248 "	7.60	0.208
18	*Alburnus alburnus*	" "	I	1	18	0.282 "	2.02	0.237
19	*Gobio gobio*	" "	I	1	18	0.281 "	63.8	0.236
20	*Leuciscus idus*	Privolnev 1947	I	C	10	~40 mg/kg/hour	650	0.075
21	" "	" "	I	C	15	~200 " "	20	0.220
22	" "	" "	I	C	15	~120 " "	118	0.188
23	" "	" "	I	C	15	~ 70 " "	815	0.110
24	*Leuciscus leuciscus baicalensis*	" "	I	C	17	~180 " "	120	0.236
25	*Phoxinus laevis*	Bounhiol 1905	II	1	18.5	0.140 ml/g/hr	4.84	0.161

Table 8 (continued)

26	Leucaspius delineatus	Yablonskaia 1951	I	C	20	0.44 mg/g/hr	1.52	0.308
27	Cobitis fossilis	Calugareanu 1907	II	5	19.3	73.88 ml/kg/hr	23.2	0.080
28	Leuciscus idus	Kharchenko 1949	I	C	20	353 mg/kg/hour	15	0.247
29	" "	" "	I	C	20	222 " "	120	0.148
30	" "	" "	I	C	20	141 " "	900	0.099
31	Leuciscus leuciscus	Mints 1952	I	5	16.5	0.36 mg/g/hr	9.95	0.342
32	Squalius cephalus	Halsband 1953	III	2	15	1.12 ml/fish/hr	14.4	0.122
33	Luxilus cornutus	Clausen 1936	III	41	18.0	131±7.1 mg/kg/hr	14.6	0.110
34	" "	" "	III	36	17.85	97±6.1 " "	20.1	0.083
35	" "	Clausen 1930	III	1	20	6.03 g/kg/day	33	0.176
36	Roach	Adrianov 1937	I	7	19.5	0.187 ml/g/hr	16.5	0.200
37	Rutilus rutilus	Ivanova 1939	I	1	18	0.285 mg/g/hr	1.75	0.240
38	" "	" "	I	1	18	0.235 " "	13.85	0.197
39	" "	" "	I	2	18	0.245 " "	39.5	0.206
40	" "	" "	I	1	18	0.130 " "	127	0.109
41	Roach	Streltsova 1953	I	1	16.5	111 ml/kg/hr	40	0.151
42	"	" "	I	2	16.5	58.3 "	222	0.079
43	Rutilus rutilus	Privolnev 1947	I	C	10	~250 mg/kg/hr	105	0.466[1]
44	" "	" "	I	C	15	~250 "	190	0.275[1]
45	Crucian carp	Adrianov 1937	I	8	19.5	0.104 ml/g/hr	60	0.109
46	" "	Ivanova 1939	I	1	18	0.133 mg/g/hr	5.2	0.112
47	" "	Veselov 1949	III	12	16	0.19 mg/g/hr	4.45	0.190
48	" "	Mints 1952	I	5	16.5	0.17 "	8.7	0.182
49	Campostoma anomalum	Clausen 1936	III	24	17.95	187±7.7 mg/kg/hr	19.25	0.157
50	Ameiurus melas	" "	III	36	17.3	73±1.9 "	49.9	0.090
	Supplement to Table 8							
51	Gasterosteus (from Gasterosteiformes)	Putter 1909	I	C	15.8	0.233 mg/fish/hr	0.716	0.330
52	Burbot (from Gadiformes)	Streltsova 1953	I	4	11.25	51.7 ml/kg/hr	213	0.121

[1] Not used in computations because it is obviously too large a figure (Fig. 34).

Table 9. [page 118] Composite table of measurements of rate of oxygen consumption of lampreys.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	*Erimyzon sucetta ollongus*[2]	Clausen 1936	III	30	18.5	153 ± 7.5 mg/kg/hr	25.8	0.123
2	*Ichthyomyzon fossor*	Leach 1946	I	5	18	0.107 ml/g/hour	3.78	0.128
3	*Petromyzon marinus*[1]	" "	I	5	18	0.129 "	3.88	0.154
4	" "	" "	I	5	22.5	0.38 "	3.44	0.308
5	" "	" "	I	5	22.5	0.23 "	3.54	0.186
6	*Lampetra fluviatilis*	Shcherbakov 1937	III	12	16.5	0.14 mg/g/hour	37	0.133

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[1] Freshwater form.

[2] [This fish, of the sucker family, belongs in Table 8. W.E.R.]

Table 10. [page 119] Composite table of measurements of rate of oxygen consumption of eels (in fresh water).

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Eel	Gardner 1926	II	C	20	56 ml/kg/hour	150	0.056
2	*Mur. anguilla*	Jolyet and Regnard 1877	II	1	14	40.5 ml/kg/hr	51.2	0.070
3	" "	" "	II	1	15.5	48.0 "	112.5	0.075
4	*Anguilla vulgaris*	Raffy 1933	I	4	13	0.0485 ml/g/hr	40	0.094
5	Eel (young)	Raffy 1933a	I	2	17	0.161 "	0.231	0.210
6	" "	" "	I	2	17	0.097 "	33	0.127
7	" "	" "	I	4	13	0.066 "	37.6	0.128
8	" "	" "	I	3	17	0.088 "	40	0.115
9	Eel ♀ (silver)	" "	I	6	17	0.091 "	54	0.119
10	Eel ♀	" "	I	?	17	0.082 "	90	0.107
11	" "	" "	I	?	17	0.069 "	430	0.090
12	Eel ♀ (silver)	" "	I	?	17	0.069 "	485	0.090
13	" " "	" "	I	?	17	0.044 "	1191	0.058
14	*Anguilla vulgaris L.*	Precht 1951	III	C	20	~ 63 ml/kg/hr	223	0.060
15	Eel	Streltsova 1953	I	6	12	24.6 "	195.5	0.053
16	"	" "	I	6[1]	14	34.5 mg/kg/hr	181.5	0.042
17	*Anguilla vulgaris*	Bounhiol 1905	II	3	18.5?	0.0875 ml/g/hr	21	0.100
18	Eel	Precht 1951	III	6	20	6.48 ml/100/g/hr	120	0.065
19	"	" "	III	C	20	6.0 "	230	0.060

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[1] Two measurements have been excluded.

Table 11. [page 120] Composite table of measurements of rate of oxygen consumption of perch and other fresh-water percoid fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Perca fluviatilis	Geyer 1939	III	3	17.4	7.5 g/kg/day	16	0.277
2	" "	Szarca 1930	III	2	20	3.96 g/kg/day	20.5	0.115
3	" "	" "	III	2	20	3.58 "	34	0.105
4	" "	Adrianov 1937	I	3	19.5	0.158 ml/g/hr	15	0.166
5	" "	" "	I	3	19.5	0.189 "	26	0.197
6	" "	Ivanova 1939	I	2	18	0.216 mg/g/hr	69.5	0.181
7	" "	Streltsova 1953	I	4	16.6	88.0 ml/kg/hr	201	0.119
8	Perca fluviatilis (fingerlings)	Lozinov 1950	III	C	24	360 mg/kg/hr	9.45	0.181
9	Perca fluviatilis (yearlings)	" "	III	C	23	270 "	19.85	0.201
10	Perca fluviatilis	Stroganov 1919	I	3	14	~110 ml/kg/hr	40	0.191
11	" "	Novikova 1939	III	2	16.75	0.135 mg/g/hr	7.45	0.126
12	" "	Novikova 1914	II	1	15.6	123.7 ml/kg/hr	15.7	0.183
13	" "	Mints 1952	I	5	16.5	0.23 mg/g/hr	11.09	0.219
14	Etheostoma blennioides	Clausen 1936	III	24	17.5	210 ± 10.8 mg/kg/hr	12.35	0.185
15	Pomoxis annularis	" "	III	36	17.4	91 ± 6.0 "	11.5	0.081
16	Huro salmoides	" "	III	48	18.3	65 ± 2.3 "	43.4	0.053
17	Acerina cernua	Ivanova 1939	I	1	18	0.195 mg/g/hr	10.4	0.184
18	" "	Streltsova 1953	I	3	17	99.4 ml/kg/hr	64.8	0.130
19	Huro floridiana	Wiebe 1933	III	8	20	5.25 ml/100/g/hr	46.75	0.052
20	" "	" "	III	8	20	6.02 "	8.8	0.060
21	Cottus gobio	Ivanova 1939	I	1	18	0.355 mg/g/hr	2.9	0.298

Table 12. [page 121] Composite table of measurements of rate of oxygen consumption of pike.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Pike	Gardner 1926	II	C	20	96 ml/kg/hour	130	0.096
2	*Esox lucius*	Lindroth 1942	I	C	15	10.0 ml/fish/hr	~250	0.063
3	" "	Privolnev 1947	I	C	10	~70 mg/kg/hr	265	0.131
4	" "	" "	I	C	15	~65 "	1850	0.072
5	*Esox lucius*, 3-year-olds	Lindstedt 1914	II	3	18.0	83.07 ml/kg/hr	280	0.100
6	" " 2-year-olds	" "	II	2	18.1	106.3 "	70.6	0.126
7	" " (spawning)	" "	II	3	13.5	51.05 "	661	0.095
8	*Esox lucius*	" "	II	1	15.0	59.7 "	680	0.094

Table 13. [page 125] Composite table of measurements of rate of oxygen consumption of cyprinodontiform fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Girardinus guppyi juv.	Raffy 1930	I	?	22	0.350 ml/g/hr	0.042	0.296
2	" " juv.	" "	I	?	22	0.399 "	0.036	0.338
3	" " males	" "	I	4	22	0.661 "	0.062	0.559
4	" " females	" "	I	2	22	0.258 "	0.404	0.218
5	" " "	" "	I	2	22	0.172 "	0.868	0.145
6	Lebistes reticulata	Smith and Everett 1943	M	35	25	0.544±18 mm^3/g/hr	0.1	0.357
7	Gambusia holbrookii	Stroganov 1939	I	C	20	0.36 ml/g/hour	0.10	0.360
8	" " males	" "	I	C	20	0.285 "	0.15	0.285
9	" " virgin females	" "	I	C	20	0.14 "	0.90	0.14
10	" " pregnant females	" "	I	C	20	0.20 "	1.50	0.20
11	G. affinis holbrookii	Maksudov 1948	I	C	27.5	0.259 mg/fish/hr	0.30	0.327
12	" "	" "	I	C	27.5	0.367 "	0.50	0.278
13	" "	" "	I	C	27.5	0.461 "	0.7	0.249
14	" "	" "	I	C	27.5	0.504 "	0.9	0.212
15	" "	" "	I	C	27.5	0.567 "	1.1	0.195
16	" "	Maksudov 1940	I	4	31	0.216 "	0.23	0.285
17	" "	" "	I	16	31	0.289 "	0.38	0.235
18	" "	" "	I	15	31	0.401 "	0.58	0.213
19	" "	" "	I	17	31	0.504 "	0.78	0.199
20	" "	" "	I	17	31	0.535 "	0.99	0.167
21	" "	" "	I	5	31	0.615 "	1.37	0.138
22	Lebistes reticulatus females	Bertalanffy 1951	–	C	20	20 mm^3/fish/hr	0.03	0.667
23	" " "	" "	–	C	20	~175 "	0.70	0.250
24	" " males	" "	–	C	20	~ 60 "	0.08	0.750
25	" " "	" "	–	C	20	~ 95 "	0.18	0.527

Table 14. [pages 130-131] Composite table of measurements of rate of oxygen consumption of various salt-water fishes, from data of Jolyet and Regnard (1877) and Bounhiol (1905).

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	Sparus auratus	Jolyet and Regnard 1877	II	1	19	142 ml/kg/hour	78.3	0.155
2	Trigla hirundo	" "	II	1	15	94.5 "	350	0.148
3	Muraena conger [Conger]	" "	II	1	13	59.8 "	545	0.116
4	" "	" "	II	1	16	75.5 "	148.3	0.108
5	Raja torpedo	" "	II	1	15	45.3 "	315	0.071
6	" "	" "	II	1	14	48.8 "	410	0.085
7	Pleuronectes solea[1]	" "	II	1	14	73.5 "	185	0.128
8	Pleuronectes maximus[2]	" "	II	1	15	80.0 "	320	0.126
9	Scyllium catulus	" "	II	1	15	54.5 "	440	0.086
10	Pipefish	" "	II	1	18	89.9 "	10.4	0.108
11	Scylliorhinus stellaris	Bounhiol 1905	II	1	18.5	0.0875 ml/g/hr	685	0.101
12	" "	" "	II	1	18.5	0.0788 "	660	0.091
13	Syngnathus acuc	" "	II	1	18.5	0.195 "	7	0.223
14	" "	" "	II	1	18.5	0.136 "	7.6	0.157
15	Conger niger	" "	II	1	18.5	0.073 "	160	0.084
16	" "	" "	II	1	18.5	0.098 "	80	0.112
17	" "	" "	II	1	18.5	0.084 "	108	0.090
18	Anguilla vulgaris[3]	" "	II	1	18.5	0.091 "	21	0.105
19	" "	" "	II	1	18.5	0.080 "	20	0.092
20	Solea vulgaris	" "	II	1	18.5	0.118 "	46	0.136
21	" "	" "	II	1	18.5	0.119 "	62	0.136
22	Barbus rhombus[4]	" "	II	1	18.5	0.091 "	145	0.105
23	" "	" "	II	1	18.5	0.134 "	50	0.155
24	" "	" "	II	1	18.5	0.102 "	70	0.118

Table 14 (continued)

25	Solea vulgaris	Bounhiol	1905	II	1	18.5	0.153	ml/g/hr	80	0.143
26	Solea vulgaris[5]	"	"	II	1	18.5	0.153	"	46	0.175
27	Platessa vulgaris	"	"	II	1	18.5	0.140	"	37	0.161
28	" "	"	"	II	1	18.5	0.129	"	28	0.149
29	Cantharus lineatus	"	"	II	1	18.5	0.179	"	407	0.206
30	" "	"	"	II	1	18.5	0.170	"	325	0.195
31	Merlangus pollachius[6]	"	"	II	1	18.5	0.198	"	155	0.227
32	" "	"	"	II	1	18.5	0.168	"	870	0.193
33	Trigla hirundo	"	"	II	1	18.5	0.095	"	350	0.109
34	Sparus auratus	"	"	II	1	18.5	0.142	"	78.3	0.163
35	Cottus scorpius[7]	"	"	II	1	18.5	0.192	"	12.3	0.221
36	" "	"	"	II	1	18.5	0.180	"	26.4	0.206
37	" "	"	"	II	1	18.5	0.181	"	24	0.208
38	" "	"	"	II	1	18.5	0.182	"	152	0.209
39	Trachinus vipera	"	"	II	1	18.5	0.200	"	10.3	0.280
40	" "	"	"	II	1	18.5	0.161	"	10.5	0.185
41	Labrus bergylta	"	"	II	1	18.5	0.192	"	57	0.220
42	" "	"	"	II	1	18.5	0.179	"	58	0.206
43	" "	"	"	II	1	18.5	0.179	"	32	0.205
44	Blennius pholis	"	"	II	1	18.5	0.235	"	13.5	0.270
45	" "	"	"	II	1	18.5	0.245	"	8.5	0.282
46	" "	"	"	II	1	18.5	0.205	"	16.5	0.236
47	" "	"	"	II	1	18.5	0.202	"	38	0.242
48	Callionymus lyra	"	"	II	1	18.5	0.230	"	13.3	0.264
49	" "	"	"	II	1	18.5	0.210	"	15.5	0.241
50	Gasterosteus marinus[8]	"	"	II	1	18.5	0.248	"	5	0.285
51	Anguilla vulgaris[3]	"	"	II	1	18.5	0.087	"	21	0.100

[1] Solea vulgaris

[2] Rhombus?

[3] A. anguilla

[4] Rh. rhombus

[5] Pl. platessa

[6] Pollachius

[7] Myoxocephalus

[8] Spinachia spinachia

Table 15. [pages 132-133] Composite table of measurements of rate of oxygen consumption of saltwater fish.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
	Order Perciformes							
1	Girella nigricans	Keys 1930	III	12	16.7	0.85 ml/g/hr	40	0.142
2	" "	" "	III	2	20.0	0.062 "	257	0.062
3	" "	" "	III	2	18.0	0.0596 "	210	0.072
4	" "	Smith 1942	III	38	20	0.131 "	70.3	0.131
5	" "	Wells 1935	?	28	20	0.196 "	5.6	0.196
6	Heliastes chromis	Vernon 1895	I	C	16	133 mg/kg/hr	10.4	0.133
7	" "	Putter 1909	I	C	22.4	4.7 mg/fish/hr	13.2	0.205
8	" "	" "	I	C	23.4	0.825 "	1.56	0.276
9	" "	" "	I	C	23.7	0.122 "	0.082	0.768
10	Serranus scriba	Vernon 1895	I	C	16	166 mg/kg/hr	4.1	0.166
11	Labrus bergylta	Baudin 1931	I	2	18	13.0 ml/fish/1 hr 45 min	125	0.071
12	Sargus rondeleti	Raffy 1933		6	14	0.186 ml/g/hr	20	0.323
13	" "	Raffy 1932	I	4	14	3.412 ml/fish/hr	25.75	0.230
14	Tautogolabrus adspersus	Haugaard 1943	M	C	20	1.65 mm^3/g/min	50	0.099
15	" "	" "	M	3	21	2.0 "	43	0.110
16	Blennius gattorugine	Baudin 1931	I	2	18	24.35 ml/fish 2 hr	98	0.124
17	" "	" "	I	3	18	11.11 ml/fish 3 hr	73	0.060
18	" "	Baudin 1931a	I	c	18	0.8 ml/fish/hr	10	0.096
19	Gobius sp.	Raffy 1933	I	3	14	0.036 ml/g/hr	20	0.062
20	Gobius paganellus	Putter 1909	I	c	23.1	2.3 mg/fish/hr	10.5	0.118
21	Cottus bubalis	Baudin 1931	I	1	20	1.63 ml/fish/hr	15	0.109
22	" "	" "	I	c	18	~0.9 ml/fish/hr	15	0.072

Table 15 (continued)

23	*Clinocottus analis*	Keys 1930	III	4	20.0	0.085 ml/g/hr	37	0.085
24	*Scorpaena porcus*	Raffy 1933	I	4	14	0.068 "	40	0.118
25	" "	Putter 1909	I	C	22.1	2.9 mg/fish/hr	16.3	0.105
	Order Cyprinodontiformes							
26	*Fundulus parvipinnis*	Keys 1930	III	10	20.0	0.212 mm^3/g/hr	5.92	0.212
27	" "	Wells 1935	III	C	20	145 "	6.34	0.145
28	" "	" "	III	C	20	250 "	2.2	0.250
29	" "	" "	III	C	20	150 "	4.8	0.150
30	" "	" "	III	4	16	0.208 ml/g/hr	0.68	0.297
31	" "	" "	III	4	16	0.145 "	1.52	0.207
32	*Fundulus heteroclitus*	Matthews 1947	III	C	21.1	~30 mm^3/fish/min	13.3	0.123
	Order Cypriniformes							
33	*Rhodeus amarus*	Raffy 1933	I	1	16	0.136 ml/g/hr	0.71	0.194
	Order Gasterosteiformes							
34	*Gasterosteus leiurus*	Raffy 1933	I	2	18	0.3 ml/g/hr	1.01	0.36
	Order Syngnathiformes							
35	*Hippocampus brevirostris*	Leiner 1937	M	4	25	508 mm^3/g/fish/hr	2.85	0.114
36	" "	" "	M	4	25	503 "	3.1	0.104
37	" "	Putter 1909	I	C	22.2	0.44 mg/fish/hr	1.75	0.146

Table 16. [page 135] Composite table of measurements of rate of oxygen consumption of marine elasmobranch fishes.

No.	Name	Author	Exptl. method	Number of expts.	T°	O_2 consumed at T°, according to the author	Fish weight, g	O_2 consumed, ml/g/hr, at 20°
1	<u>Sc. catulus</u>	Jolyet and Regnard 1877	II	1	15	54.5 mg/kg/hour	440	0.0855
2	<u>Scylliorhinus stellaris</u>	Bounhiol 1905	II	1	18.5	0.0875 mg/g/hr	685	0.101
3	" "	" "	II	1	18.5	0.0788 "	660	0.091
4	<u>Scyllium catulus</u>	Raffy 1932	I	3	14	2.077 ml/fish/hr	24	0.151
5	" "	" "	I	3	14	1.474 "	18.95	0.135
6	<u>Scyllium cassicula</u>	Buytendijk 1910	I	1	13[1]	0.87 ml/fish/hr	14	0.121
7	" "	" "	I	1	13	1.26 "	24	0.102
8	" "	" "	I	1	13	4.9 "	150	0.063
9	" "	" "	I	1	13	8.16 "	215	0.073
10	" "	" "	I	1	13	9.63 "	260	0.072

[1] Temperature approximate, from data of preliminary experiments.

Table 17. [page 138] Calculated expected metabolic rates of various fishes at weights of 1 g and 1 kg.

	O_2 consumption			
	ml/g/hour at 20°		% of the mean	
Name of fish	1 g	1 kg	1 g	1 kg
Sturgeons	0.391	0.105	109	114
Salmonoid fishes	0.498	0.095	138	103
Cyprinid fishes[1]	0.336	0.084	93	91
Carp	0.343	0.122	95	133
Tench	0.230	0.054	64	59
Mean	0.360	0.092	100	100

[1] Excluding carp, goldfish and tench.

Table 18. [page 139] Composite table of parameters of the parabolic equations relating metabolism and body weight of various fishes, computed by the method of least squares.

Equation No.	Name of fish	n	σ_y	σ_x	r	Σ_y	log a	a	$k \pm \sigma_k$
5.3.1	Goldfish	22	0.49	0.58	0.948	0.151	-0.759	0.174	0.81 ± 0.060
5.4.1	Carp	35	1.13	1.35	0.997	0.087	-0.465	0.343	0.85 ± 0.012
6.1.1	Acipenserid fishes	33	1.43	1.75	0.997	0.111	-0.408	0.391	0.81 ± 0.010
6.1.2	Salmonid fishes	30	0.93	1.20	0.976	0.203	-0.303	0.498	0.76 ± 0.032
6.1.3	Tench	17	0.54	0.68	0.965	0.141	-0.638	0.230	0.79 ± 0.051
6.1.4	Freshwater cyprinid fishes[1]	50	0.63	0.74	0.935	0.223	-0.473	0.336	0.80 ± 0.044
6.1.5	Cyprinodont fishes	25	0.38	0.52	0.963	0.102	-0.717	0.192	0.71 ± 0.042
6.1.6	All freshwater fishes (Tables 3-13)	266	0.99	1.19	0.969	0.077	-0.528	0.297	0.81 ± 0.014
6.2.1	Marine fishes (Table 14)	51	0.55	0.61	0.968	0.144	-0.575	0.266	0.87 ± 0.032
6.2.2	" " (Table 15)	37	0.65	0.72	0.882	0.304	-0.649	0.224	0.80 ± 0.072
6.2.3	Young marine fish, after Zeuthen	25	0.67	0.86	0.907	0.282	-0.484	0.328	0.71 ± 0.067
6.2.4	All marine fishes (including Table 16)	123	1.05	1.30	0.969	0.259	-0.493	0.321	0.79 ± 0.014
7.3.1	All fish	389	1.01	1.23	0.974	0.228	-0.500	0.316	0.78 ± 0.0096
7.3.2	All fish except (6.2.3)	364	0.93	1.11	0.971	0.222	-0.545	0.285	0.81 ± 0.0105

Legend: n—number of initial data according to Tables 3-16.
σ—mean square deviation.
$y = \log Q$; Q—total metabolism, ml O_2/fish/hr at 20°.
$x = \log w$; w—weight of 1 fish in g.

r—correlation coefficient.
$a = Q$ at $w = 1$; $Q = aw^k$.
$\Sigma_y = \sigma_y \sqrt{1-r^2}$.

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[1] Other than goldfish, carp and tench.

Table 19. [page 153] Table of approximate values of the routine metabolism of fish, calculated from the equation $Q = 0.3\ w^{0.8}$

Weight of fish, mg	Q	$\frac{Q}{w}$	cal	Weight of fish, g	Q	$\frac{Q}{w}$	cal	Weight of fish, kg	Q	$\frac{Q}{w}$	cal
1	0.0012	1.19	143	1	0.300	0.300	36	1	75	0.075	9.0
3	0.0029	0.96	115	3	0.723	0.24	29	3	182	0.061	7.3
10	0.0075	0.75	90	10	1.89	0.19	23	10	475	0.047	5.6
30	0.0182	0.61	73	30	4.56	0.15	18	30	1146	0.038	4.6
100	0.0475	0.47	56	100	11.94	0.12	14	100	3000	0.030	3.6
300	0.1146	0.38	46	300	28.8	0.096	11.5				

Q—consumption of O_2 by 1 fish, in ml per hour at 20°.

$\frac{Q}{W}$ -metabolic rate (ml O_2/g/hr at 20°).

cal—energy expenditure in routine metabolism, in cal/g/day at 20°.

Table 20. [page 180] Energy expenditures by fish in motion.

Name of fish	Average weight of fish, g	Speed of motion, m/sec	T°	Active metabolism / Resting metabolism	Energy expenditure cal/g	
					per hour	per km of movement
Chum salmon, males	5033	1.33	12	> 8	1.075	0.225
Chum salmon, females	3955	1.33	12	> 8	1.183	0.249
Salvelinus fontinalis	27	0.8	15	4	1.400	0.486
Goldfish	3.8	0.5	24	2	0.575	0.320
Salvelinus namaycush[1]	27.7	0.53	16	6.5	1.2	0.623
" " [1]	82.8	0.66	16	5.5	1.2	0.504

[1] According to data in Fig. 2 and 6 of Gibson and Fry (1954).

Table 21. [page 190] Average daily gain in weight of young fish in the brood ponds of two Belorussian fish farms, estimated from daily observations and from computations by formula (10.2.1) using the initial and final weight.

Name of fish farm	Year of observation	Observation period	Average final weight of 1 specimen	Average daily gain in weight	
				Observed	Computed
		days	mg	%	%
Volma	1951	15	24.7	21	21
"	"	15	33.9	23	21
"	"	15	16.5	17	19
"	"	15	24.7	17	20
"	1950	19	27.4	14	15
"	"	19	41.1	18	19
Slepîanka	1946	9	27.6	45	42
"	"	19	101.6	31	28

Remark: The growth of young fish at the Volma Pond-fish Farm is from data of the Belorussian division of VNIORKh, that for the Slepîanka farm is from data of G. V. Gladky. The observations in all cases were begun on the 3rd day after hatching, and the initial weight of the fish was 1.5 mg.

Table 22. [page 192] Average daily gain in weight of young fish of various species during their initial period of development.

Species of fish, and author's name	Days from start of observations	Average weight of a young fish	Average daily increase in weight	
			According to the author	From formula (10.2.1)
	days	mg	%	%
WILD CARP (Krivobok, 1953)	0	3.2	144.3	52.5
	5	26.3	86.4	37.5
	10	140.0	33.3	17.5
	19	560.0	3.1	4.7
	27	700.0		
BREAM (Letichevsky, 1953)	0	3.0	106.3	30
	9	31.68	33.27	14.5
	20	137.11	2.91	2.6
	30	177.11	7.52	6.2
	40	310.34		
VOBLA (Tarkovskai͡a, 1953)	0	3.11	235.2	57.8
	6	47.0	14.59	10.7
	13	95.0	6.17	5
	24	159.5	5.16	5
	36	274.9		
DOMESTIC CARP (Konstantinov, 1953)	0	2.08	24.0	15
	6	4.9	11.2	7.5
	18	11.5	7.0	5.5
	29	20.4		

[page 214]

Table 23. Growth rate, food consumption and metabolic rate of young wild carp, from data of Krivobok (1953).

Periods of observation	Mean weight of 1 fish in grams wet weight	Mean T°	Daily weight gain in % (dry weight)	Daily ration in % (dry weight)	Coefficient of utilization (K_1)	Expenditure for metabolism per day, as % (dry weight)	Metabolic rate as ml O_2/g wet wt./hr		
							Calculated	Expected	Measured
16.v-21.v	0.0147	21.8	31.4	54.1	58.0	11.9	0.60	0.81	0.77
21.v-26.v	0.083	21.5	28.3	48.0	59.0	10.1	0.54	0.56	0.61
26.v-4.vi	0.350	22.2	13.7	28.8	47.5	9.3	0.54	0.45	0.65
4.vi-12.vi	0.630	25.9	5.03	15.6	32.2	7.4	0.49	0.53	0.63
12.vi-26.vi	1.105	28.7	7.06	13.9	50.7	4.1	0.31	0.61	0.67
26.vi-14.vii	1.985	28.1	2.42	11.5	21.0	6.8	0.54	0.50	0.58
14.vii-28.vii	2.566	24.7	0.96	8.2	11.8	5.6	0.45	0.37	0.38
28.vii-14.viii	2.802	24.7	0.72	6.5	11.1	4.5	0.38	0.36	0.36

Table 24. [page 216] Growth rate, food consumption and metabolic rate of 4-year-old roach (from data of G. S. Karzinkin, 1952).

Period of observations	Mean weight of 1 fish in grams wet weight	Mean T°	Mean daily weight gain, as % (cal)	Mean daily ration, as % (cal)	Coefficient of utilization (K_1)	Expenditure for metabolism per day, as % (cal)	Metabolic rate as ml O_2/g wet wt./hr	
							Calculated	Expected
26.v-11.vi	20.50	20.4	0.93	5.60	16.6	3.51	0.27	0.17
11.vi-26.vi	21.85	23.5	0.57	5.95	9.5	4.07	0.32	0.22
26.vi-11.vii	22.35	21.8	0.46	4.94	-	4.43	0.37	0.19
11.vii-26.vii	23.05	20.0	1.49	3.33	44.7	1.17	0.09	0.16
26.vii-1.viii	24.50	20.2	0.60	4.51	13.3	3.01	0.30	0.18
11.viii-24.viii	25.55	20.5	0.08	4.30	2.0	3.36	0.33	0.16
Mean			0.54	4.77	11.3[1]	3.26	0.28	0.18

[1] Computed from the mean values of the two previous columns.

Table 25. [page 218] Growth rate, food consumption and metabolic rate of carp (from data of Ivlev, 1939).

Period of observations	Mean weight of 1 fish in grams wet weight	Mean T°	Mean daily weight gain, as % (cal)	Mean daily ration, as % (cal)	Coefficient of utilization in % (K_1)	Mean daily expenditure for metabolism, as % (cal)	Metabolic rate as ml O_2/g wet wt./hr	
							Calculated	Expected
19.v-4.vi	24.4	18.0	5.16	12.3	42	4.7	0.36	0.13
4.vi-19.vi	56.0	15.5	5.61	11.3	50	3.4	0.28	0.09
19.vi-4.vii	96.5	19.8	2.90	9.8	30	4.9	0.37	0.12
4.vii-19.vii	171.0	23.6	5.69	12.3	46	4.2	0.41	0.15
19.vii-4.viii	280.0	22.6	2.42	9.3	26	5.0	0.53	0.13
4.viii-19.viii	363.0	21.0	1.33	4.8	28	2.5	0.27	0.12
19.viii-1.ix	407.5	18.3	0.90	4.9	18	3.0	0.14	0.10

Table 26. [page 220] Growth rate, food consumption and metabolic rate of *Leucaspius delineatus* (from data of E. A. Yablonskai͡a, 1951).

Period of observations		Mean weight of 1 fish in grams wet weight	Mean T°	Mean daily weight gain as % (dry weight)	Mean daily ration, as % (dry weight)	Coefficient of utilization (K_1)	Mean daily expenditure for metabolism, as % (dry weight)	Metabolic rate as ml O_2/g wet wt./hr		
								Calculated	Expected	Measured
24.vii-1.viii	females	1.64	23	0.69	14.5	4.8	10.9	0.91	0.35	0.33
"	males	1.45	23	0.56	15.0	3.7	11.4	0.99	0.36	
1.viii-26.viii	females	1.71	20	0.80	10.9	7.3	8.0	0.70	0.27	0.30
"	males	1.46	20	0.51	9.9	5.2	8.4	0.79	0.28	
26.viii-10.ix	females	1.77	16	0.17	5.7	3.0	4.4	0.41	0.19	0.24
"	males	1.49	16	0.48	5.8	8.3	4.1	0.38	0.19	

[1] From the temperature of the measurements of O_2 utilization.

[2] The dry weight of the males for 1.viii-26.viii was obtained by interpolation between the weights for 24.vii and 10.ix.

Table 27. [page 222] Growth rate, food consumption and metabolic rate of young inconnu (from data of Karzinkin, 1952).

Period of observations	Mean weight of 1 fish in grams wet weight	Mean T°	Daily weight gain in % (dry weight)	Daily ration in % (dry weight)	Coefficient of utilization (K_1)	Daily expenditure for metabolism in % (dry weight)	Metabolic rate as ml O_2/g wet wt./hr	
							Calculated	Expected
5-20.iv	0.0247	18.5	11.9	25.7	46.2[1]	8.7	0.49	0.55
29.iv-9.v	0.151	18.5	14.1	23.4	60.2	4.6	0.29	0.38
9.v-19.v	0.456	19.0	9.8	24.5	40.1[2]	9.8	0.68	0.32

[1] Erroneously given as 52.6% in table 88 of Karzinkin's book.

[2] Erroneously given as 35.4% in the same table.

Table 28. [page 222] Growth rate, food consumption and metabolic rate of young osëtr (from data of Karzinkin, 1952).

Age in days from the activity of feeding	Mean weight of 1 fish in grams wet weight	Mean T°	Daily weight gain in % (dry weight)	Daily ration in % (dry weight)	Coefficient of utilization (K_1)	Daily expenditure for metabolism in % (dry weight)	Metabolic rate as ml O_2/g wet wt./hr	
							Calculated	Expected
3-11	0.101	16.0	13.5	34.3	39.4	13.9	0.64	0.33
11-21	0.378	17.6	12.1	27.8	43.5	10.1	0.46	0.29
21-31	1.216	19.6	10.9	26.4	41.7	10.2	0.51	0.28
31-36	2.335	21.5	8.4	25.1	33.5	11.7	0.61	0.29
74-81	17.08	22.6	2.3	5.64[1]	41.0	2.2	0.15	0.21

[1] Erroneously given as 5.2 in table 45 of Karzinkin's book.

Table 29. [page 223] Growth rate, food consumption and metabolic rate of young pike (apparently the data concerning food rations are inaccurate, see page 224 of the text) (from data of Karzinkin, 1952).

Age in days from the activity of feeding	Mean weight of 1 fish in grams wet weight	Mean T°	Daily weight gain in % (dry weight)	Daily ration in % (dry weight)	Coefficient of utilization (K$_1$)	Expenditure for metabolism per day, as % (dry weight)	Metabolic rate as ml O_2/g wet wt./hr	
							Calculated	Expected
FED DAPHNIA								
9	0.0348	18-25	23	115.0	20.0	69	2.71	0.59
19	0.1369	"	16.2	75.0	21.6	43.8	2.57	0.45
29	0.438	"	11.8	58.7	20.1	35.2	2.24	0.35
39	1.053	"	7.8	31.3	25.0	17.2	1.15	0.30
62	2.530	"	2.8	12.5	22.4	7.2	0.56	0.25
79	3.157	"	1.0	4.7	21.5	2.8	0.22	0.24
FED YOUNG FISH								
23	0.136	18-25	19.8	99.3	19.9	59.6	3.56	0.45
31	0.436	"	15.2	40.2[2]	-	-	-	-
41	1.379	"	10.8	40.4	26.7	21.5	1.50	0.28

[1] Expected metabolism for 20°.

[2] Clearly too low a figure.

Table 30. [page 229] Computed values of daily weight increase and rations, for various coefficients of utilization of food for growth, by fish of various sizes.

Weight of fish in grams wet weight	Provisional maximal expenditure for metabolism, as % of weight	Daily rations as percentage of weight			Daily weight gains as percentage of weight		
		$K_2 = 60$ $K_1 = 48$	$K_2 = 20$ $K_1 = 16$	$K_2 = 5$ $K_1 = 4$	$K_2 = 60$ $K_1 = 48$	$K_2 = 20$ $K_1 = 16$	$K_2 = 5$ $K_1 = 4$
0.001	28.6	89.5	44.7	37.6	43	7.1	1.50
0.01	18.0	56.3	28.2	23.7	27	4.5	0.95
0.1	11.3	35.4	17.7	14.9	17	2.8	0.59
1.0	7.2	22.5	14.8	9.5	10.8	2.4	0.38
10	4.6	14.4	7.2	6.0	6.9	1.15	0.24
100	2.9	9.1	4.5	3.8	4.4	0.72	0.15
1000	1.8	5.6	2.8	2.4	2.7	0.45	0.09

Table 31. [page 232] Average monthly temperatures at depths preferred by trout in Lake Sevan.

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Temperature	5[1]	5[1]	5[1]	5[1]	6.5	12	15	15	15	14	10.5	6.5
Coefficient	5.19	5.19	5.19	5.19	4.26	2.16	1.57	1.57	1.57	1.74	2.54	4.26

[1] For the winter months a temperature exceeding the one prevailing in the lake has been taken deliberately. In this way we have attempted to take into consideration the increase in metabolic level that results from adaptation to low temperatures, which must occur in Sevan trout, since they are active during the winter.

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+ 4 tables

TABLE 32. [page 234] Annual rations and food coefficients of the Sevan trouts, computed from the Expected magnitude of their metabolism and from the values given by Dadikîan in his quantitative study of feeding (data from Dadikîan, 1955).

Race of trout	Age	Mean weight g	Annual increase in weight, g	Computed annual ration, thousands of calories	Food coefficient	
					Computed	From Dadikîan
Gegarkuni	2+	84	70	256-425	5.40-8.98	6.5
"	3+	177	117	452-758	5.71-9.58	10.2
"	4+	298	124	620-1083	7.40-14.7	13.7
"	5+	418	117	756-1368	9.56-17.3	24.8
"	6+	561	168	980-1751	8.64-15.4	24.0
Bodzhak	3+	110	41	261-500	9.4-18.1	17.3
"	4+	142	22	285-541	19.2-36.4	41.5
"	5+	171	35	342-639	16.4-27.0	44.7
"	6+	211	47	411-764	14.7-24.1	41.1

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