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by A. S. Konstantinov

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1. Connection between the Gas Exchange and the Temperature.

By A.S. Konstantinov.

(From: "Biologiya khironomid i ikh razvedeniye." /Biology of chironomids and their cultivation/, "Trudy Saratovskogo otdela VNIORKh." /Transactions of the Saratov Branch of the All-Union Research Institute of the Lake and River Fisheries/, Vol. 5, p. 91 - 108, 1958).

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Studies of Vinberg (1939) and Gorodetskaya (1948) have shown that the respiration intensity of the chironomid larvae depends on the thermal conditions under which the animals lived prior to the experiment. Our research on the role of the temperature factor in the respiration of the chironomids was started with the study of these peculiarities, which are of methodological importance.

The determination of the role of the temperature conditions under which the animals were kept prior to the experiment was carried out on the Ch. dorsalis larvae, whose gas exchange was measured by means of a Warburg apparatus. The weight of the assay larvae was three milligrams, the temperature during the measurement of their respiration was 21°C. The following data were obtained: /p. 92

Temperature of water, in which the larvae were kept prior to the experiment	1°	11°	21°	30°
Intensity of O_2 consumption during the experiment (in milligrams per one gram of raw weight per hour) ..	0.48	0.76	0.50	0.86

As we see from the presented data the increase in gas exchange in the Ch. dorsalis larvae is observed during the experiment, in the case of a pre-experimental effect of both low (11°C) and high (30°C) temperatures. This increase is probably connected with the increase in the activity of animals moved to an acutely different thermal environment. Indeed, transfer of animals from cold (11°C) and from warm (30°C) water into manometric flasks is accompanied by a much more energetic and prolonged swimming, than in the case of larvae transferred into vessels from thermal conditions similar to those in the Warburg apparatus (21°C).

It is characteristic that animals, kept prior to the experiment in the coldest water (1°C), did not manifest any increase in respiration intensity as compared to the control animals (21°C). Apparently, the respiration level in larvae at 1°C is very low, and although the level rises rapidly when the latter are transferred to warm water (21°C), however, owing to a considerable inertia of the organism it has no time to reach any high average values.

Taking the obtained results into consideration, further studies on respiration were carried out on animals, which prior to the experiment were kept for a period of 12 to 15 hours under the same thermal conditions, as the ones under which the intensity of their respiration was to be measured according to the experiment. The measurement of the gas exchange was carried out according to the flask method. Larvae of comparable size (weight) were used in the experiments, they were collected simultaneously from the ground. Three to ten larvae (depending on their weight) were placed in the flasks with a volume of 70 to 80 millilitres and filled with properly aerated water (8 to 9 milligrams of O_2 per litre). The duration (exposure) of the experiment usually was five hours, the difference in the content of oxygen during the observations did not, as a rule, exceed 1 to 1.5 milligrams per litre. The determination of oxygen was conducted in vessels with a volume of ten millilitres, two, sometimes three, determinations were carried out side by side.

Oxygen content in the flasks was measured as control prior to the experiment and after the same; results of the latter determination were used in the calculations.

In the first series of the experiments (table 30) we studied the effect on the temperature of the gas exchange in larvae of same species (Ch. dorsalis), but of different size. It was established that the data from individual measurements differ rather considerably (sometimes by twice or more) from each other, and therefore only an average of many observations can be taken as index of the exchange level (we took an average of 8 to 11 measurements). A considerable discrepancy in the results of individual experiments is caused by the impossibility of standardizing the behaviour of /p. 93 highly organized animals, which in individual cases manifest different degrees of activity. We considered it inacceptable to narcotize the larvae, because the more standard results obtained under such conditions would be without any practical value. To disregard the effect of the temperature factor upon the nervous system, would have meant that we would study a reaction to changes not in real, but in abstract animals, in other words, we would be producing data without any practical value.

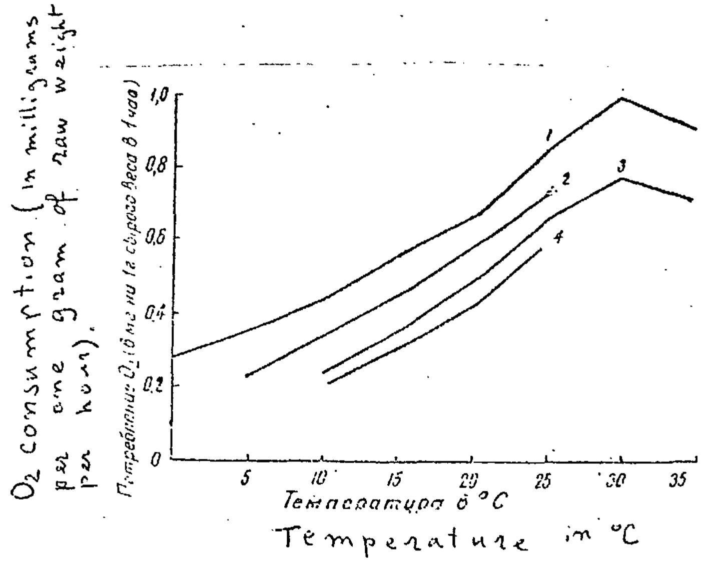


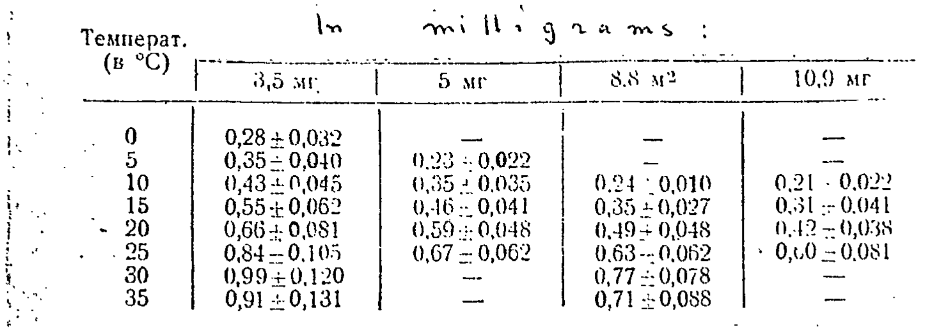
Fig. 8 Oxygen consumption by Chironomus dorsalis larvae weighing 3.5 milligrams (1), 5 milligrams (2), 8.8 milligrams (3) and 10.9 milligrams (4) under various temperature conditions.

Graphic presentation of the data shown in table 30 permits us to see that the respiratory reaction of animals of different size to changes in temperature is practically uniform. In all cases the curves of the oxygen consumption (fig. 8) are almost /p. 94 parallel to each other, although running at different levels. The latter fact, as we will prove later in the text, reflects the age peculiarities of the gas exchange in animals and is not connected to the differences in their reaction to the temperature changes.

Table 30

The value of oxygen consumption by Ch. dorsalis larvae of various size under various temperature conditions.

Temperature (in °C)	O_2 consumption (in milligrams per one gram of raw weight per hour) in larvae of different weight (M ± m)



Температ. (в °C)	In milligrams : 3,5 мг	5 мг	8,8 мг	10,9 мг
0	0,28 ± 0,032	—	—	—
5	0,35 ± 0,040	0,23 ± 0,022	—	—
10	0,43 ± 0,045	0,35 ± 0,035	0,24 ± 0,010	0,21 ± 0,022
15	0,55 ± 0,062	0,46 ± 0,041	0,35 ± 0,027	0,31 ± 0,041
20	0,66 ± 0,081	0,59 ± 0,048	0,49 ± 0,048	0,42 ± 0,038
25	0,84 ± 0,105	0,67 ± 0,062	0,63 ± 0,062	0,60 ± 0,081
30	0,99 ± 0,120	—	0,77 ± 0,078	—
35	0,91 ± 0,131	—	0,71 ± 0,088	—

As we see from fig. 8, the changes in the temperature and in the respiration intensity are connected by a practically rectinlinear function within the range of 10 to 25°C. When the temperature drops from 10 to 1°C, or rises from 26 to 30°C, the rate in the change of the respiration intensity decelerates, when the temperature rises above 30°C, then the absolute respiration value decreases. In practice, the rectilinear character of the relation between the gas exchange and the temperature, within the latter's limits of 10 and 25°C, allows us to set up a simple interpolation formula of the connection between the two values in Ch. dorsalis larvae of various sizes. Evidently, it will be expressed by a rectilinear equation:

$$y = a + bx,$$

where y is the value of the gas exchange, x is the temperature, a and b are constants.

By finding the constants from the formulae:

$$a = \frac{y_1 x_2 - y_2 x_1}{x_2 - x_1}$$

$$b = \frac{y_2 - y_1}{x_2 - x_1}$$

we obtain the following values for these constants:

weight of larvae in milligrams	3.5	5	8.8	10.9
value of constant a ..	0.13	0.08	-0.07	-0.13
value of constant b ..	0.041	0.043	0.042	0.042

By comparing the calculated values of the constants, we see that there is a similarity between a change in the gas exchange and an increase in the temperature in larvae of all the studied sizes, and, furthermore, between a regular increase in the level of curves and a decrease in the weight of animals.

The value of the angular coefficient (constant b) in individual equations fluctuates between 0.041 and 0.043, and is 0.042 on the average. The value of the initial ordinate (constant a) is in a negative rectilinear relation to the weight of animals, and may be determined by the equation:

$$a = 0.24 - 0.35P,$$

where P is the weight of larvae in milligrams.

Thus, the respiration intensity of the Ch. dorsalis larvae of any size may be found within the temperature interval of 10 to 25°C according to the equation:

$$y = (0.24 - 0.035P) + 0.042T,$$

where y is the value of the respiration (in milligrams of 0_2 per one gram of raw weight per hour),

P is the weight of larvae in milligrams,

T is the temperature in °C. /p. 95

In table 31 are shown data on respiration, at various temperatures, in seven species of chironomid larvae, some of which (representatives of the genera Chironomus and Glyptotendipes) belong to the thermophylic forms, and some (S. nivosa, P. olivacea) to the psychrophylic ones. The presented figures are mean values of seven to ten measurements, the average error m is, as a rule, 8 to 12% of M, in individual cases, it is as high as 15 to 18%.

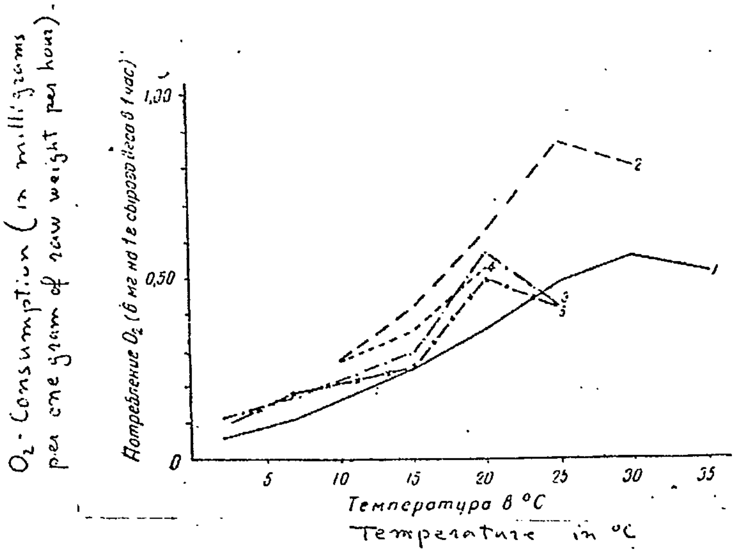


Fig. 9. Oxygen consumption by Chironomus plumosus larvae (1), Ch. annularis larvae (1), Ch. annularius larvae (2), Prodiamesa olivacea larvae (3), Glyptotendipes pallens larvae (4) and Syndiamesa nivosa larvae (5) under different temperature conditions.

Table 31.

The value of the oxygen consumption by some chironomid larvae under different temperature conditions.

Species	Weight of one individual (in milligrams)	Consumed O₂ (in milligrams per one gram of raw weight per one hour) at various temperatures.							
		2°	7°	10°	15°	20°	25°	30°	35° C.
Ch. plumosus	25	0,07	0,11	—	0,25	0,35	0,48	0,54	0,51
Ch. annularius	7	—	—	0,26	0.42	0,64	0,86	0,80	—
Ch. heterodentatus	3	—	—	0,40	0,52	0,73	0,89	0,79	—
G. pallens	8	—	—	0,27	0,35	0,52	—	—	—
E. tendens	4	—	—	0,41	0,49	0,61	0.64	0,61	—
S. nivosa	10	0,10	0,18	—	0,25	0,49	0.41	—	—
P. olivacea	6	0,11	0,17	—	0,29	0,56	0,42	—	—

It is easy to see that the effect of temperature upon the gas exchange varies from species to species. Thus, the absolute oxygen consumption per one unit of raw weight both in Ch. plumosus, and in Ch. dorsalis, decreases when the temperature rises above 30°C. /p. 96

In other thermophylic forms this critical point is in the environment of 25 to 30°C, in the cold-resistant forms this point is around 20°C. When compiling the tabular material into a graph (fig. 9) other differences are also clearly noticeable. Thus, the range of approximately rectilinear relation between the gas exchange and the temperature for Ch. plumosus is within the limits of 4 and 27°C, in the case of Ch. annularius the upper boundary of this range attains 25°C, in P. olivacea and S. nivosa the rectilinear connection of the discussed values is observed only in the interval ranging from 2 to 17.5°C.

It is interesting to note, that the Ch. plumosus and Ch dorsalis react to a temperature increase above certain limits initially with a decrease in the rate of the acceleration in respiration, then with a decrease in the absolute indices in the gas exchange. S. nivosa and P. olivacea react differently: first the intensity of respiration increases rapidly, and only then starts the depression in the process.

The general pattern apeears on the background of the differences in the reactions in different species. In all the instances the change in temperature within certain limits corresponds to a proportional shift in the respiration value. In all the instances a change in temperature corresponds within certain limits to a proportional shift in the respiration value. Beyond the limits of this section of practically rectilinear relation the proportionality in the respiration change in relation to the temperature is disrupted. The length of the section of the rectinlinear relation and its absolute boundaries are different in different species and are, apparently, reflecting biological peculiarities of the animals. It is most probable, that the centres of the rectilinear sections of the curves of the gas exchange correspond to the conditions of the thermotactical optimum for the larvae. Thus, the rectilinear relation between the temperature and the gas exchange in the Ch. plumosus larvae is observed within the limits of 4° and 27°C, the middle of this interval equals:

$$\frac{4^{\circ} \neq 27^{\circ}}{2} = 15^{\circ}\mathrm{C}.$$

Almost a completely identical temperature (15.5°C) is indicated by Zabolotsky (1939) on the basis of direct measurements as being the thermotactical optimum for the discussed form.

In the case of the P. olivacea larvae, according to our data, the range of rectilinear connection of the temperature and of the respiration is located in the interval of 2 to 17.5°C, the middle of the interval is:

$$\frac{2^{\circ} \neq 17.5^{\circ}}{2} = 9.75^{\circ}\mathrm{C}.$$

According to Zabolotsky the thermotactical optimum for the P. olivacea larvae is 10.8°C. Unfortunately, the thermotactical optimum is unknown for the other forms studied by us.

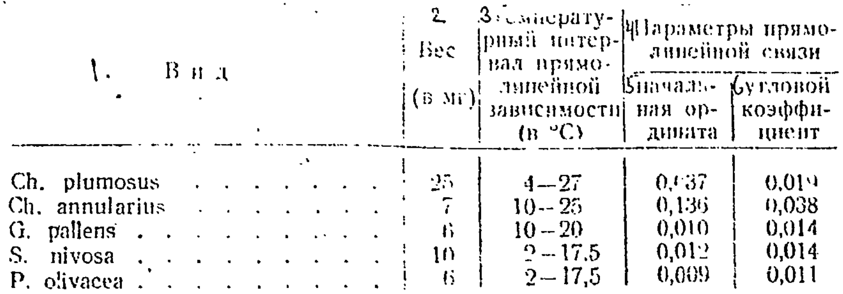
By studying (practically) the middle of an interval of the rectilinear relation between the gas exchange and the temperature corresponding to the thermotactical optimum for the animals, we see the characteristics of their eurythermality in the size of the interval. /p. 97

The narrower the mentioned interval is, the less eurythermal is the form, and the narrower are the temperature limits within which the control mechanisms may operate successfully ensuring the coordinated reaction of the entire organism to a change in the external conditions.

As our data show, the interval of the practically rectilinear relation between the gas exchange and the temperature in the eurythermal forms has greater length, than in the stenothermal species not merely in the absolute expression, but in the relative respect. Let us mention, as illustrated, that the temperature range of the existance of the Ch. dorsalis larvae is by 6° wider than the same of P. olivacea (Konstantinov, 1955; Walsh, 1948), but the interval of the rectilinear connection of the gas exchange with the temperature is by 10° wider. Thus, the temperature adaptation of the animals takes place, apparently, both because of the absolute, and because of the relative extension of the thermal zone within the limits where the respiration of the larvae is not suppressed.

Table 32.

The range and parameters of the rectilinear relation between the temperature and the gas exchange in certain chironomid larvae.



1. Вид	2. Вес (в мг)	3. Температурный интервал прямолинейной зависимости (в °C)	4. Параметры прямолинейной связи	
			5. Начальная ордината	6. Угловой коэффициент
Ch. plumosus	25	4–27	0,037	0,019
Ch. annularius	7	10–25	0,136	0,038
G. pallens	6	10–20	0,010	0,014
S. nivosa	10	2–17.5	0,012	0,014
P. olivacea	6	2–17,5	0,009	0,011

Captions in the table:

1. Species
2. Weight (in milligrams)
3. Temperature interval of rectilinear relation (in °C)
4. Parameters of the rectilinear relation:
5. initial ordinate
6. angular coefficient

Table 32 shows intervals for individual chironomid larvae, in which the relation between the temperature and the gas exchange is practically rectilinear, the parameters of the rectilinear relation are also shown. The parameters are shown for the equation $y = a + bx$, where y is the value of the gas exchange in the larvae in milligrams of O_2 per one hour per one gram of raw weight, x is the temperature in ^{o}C. Often, in the practice and in the research work, it is necessary to know the temperature corrections to bring the values of gas exchange to a certain temperature. For this purpose the coefficient Q10 is often used, this often leads to considerable errors, since the values of the mentioned coefficient are rather dissimilar at different sections of the temperature range. The data shown in table 32 permit us to obtain an equation of the relation between the values of the gas exchange at different temperatures. /p. 98

If we plot the temperatures along the abscissa axis, and along the ordinate axis we plot the values of the respiration of the larvae, i.e. values referred to the gas exchange at any constant temperature (for example 10°C), then we will obtain a number of straight lines that may be expressed by the equation:

$$\frac{y_1}{y} = 1 + K(t_1 - t), \tag{1}$$

where y_1 is the value of respiration at the temperature t_1,

y is the same at the temperature t (in our case 10°C),

K is a constant.

By multiplying both sides of the equation by y, we have:

$$y_1 = y/1 + K(t_1 - t)/. \tag{2}$$

If we take as the initial value a level of gas exchange at the temperature 10°C, then it is evident that:

$$y_1 = y/1 + K(t_1 - 10)/, \quad \text{or}$$

$$y = \frac{y_1}{1 + K(t_1 - 10)} \tag{3}$$

The gas exchange level at temperature $\underline{t}_2$ may, evidently, be calculated according to the equation:

$$y_2 = y/1 \not- K(t_2 - 10)/.$$

By substituting into this equation the value $\underline{y}$ from equation (3), we have:

$$y_2 = \frac{y_1 \ /1 \not- K(t_2 - 10)\ /}{1 \not- K(t_2 - 10)}, \tag{4}$$

where $\underline{y}_2$ is the sought level of gas exchange for temperature $\underline{t}_2$,

$\underline{y}_1$ is the level of the gas exchange in larvae determined for temperature $\underline{t}_1$.

The equation (4) permits us to calculate the value of the gas exchange of the animal for one or another temperature (in the earlier indicated intervals), if we know the value of the respiration at any other temperature and if we know the constant K.

The latter is numerically equal to the angular coefficient of the change curves for the respiration intensity, referred to the respiration level at 10°C, and for the studied larvae it is expressed by the following values:

Ch. dorsalis...............	weight:	3.5 milligrams	(2.5 - 25°C) - 0.055
"	"	5.0 milligrams	(5 - 25°C) - 0.092
"	"	8.8 milligrams	(10 - 25°C) - 0.140
"	"	10.9 milligrams	(10 - 25°C) - 0.180
Ch. plumosus...............	"	25.0 milligrams	(5 - 25°C) - 0.120
Ch. annularius	"	7.0 milligrams	(10 - 25°C) - 0.140

G. pallens	weight:	6.0	milligrams	(10 - 20°C) - 0.060
S. nivosa	"	10.0	"	(2 - 15°C) - 0.052
P. olivacea	"	6.0	"	(2 - 15°C) - 0.069

The pattern of the increase in the shown constant for the Ch. dorsalis larvae, when the live weight of the animal is increased, is noticeable. As the calculations have shown, this connection between the value of the constant and the weight of the animals is expressed by the rectilinear equation:

$$K = 0.013 + 0.0145P,$$

where P is the weight of the larvae in milligrams. /p. 99

This means that the change in the intensity of respiration with the increase in temperature is higher, the older (larger) the organism is. In other words, the value of the temperature coefficient (Q10), which is extensively used in biology, is directly proportional to the animal's age.

It is well known, that Beleradek (1926), on the basis of the concept of the temperature effect upon the speed, with which the biological processes are taking place through change in the diffusion rate, believed that the temperature coefficient is the higher, the older the organism is (increase in the viscosity of biocolloids). Although the theoretical hypotheses of Beleradek were subjected to serious criticism and it was proved in a number of experiments (Bodine, 1921), that the experimental dehydration of the albumens is not accompanied by an increase in the temperature coefficient, the fact of its increase with the growth has obtained new confirmations. It is probable, that we can also interpret our data in this aspect. Let us mention, that Yeltsina (1940), while denouncing in toto the hypotheses of Beleradek, considers them probable if applied in one special case, namely, respiration.

Study of the thermal effects upon the intensity of respiration of the chironomids indicates convincingly the impossibility of finding universal quantitative patterns of changes in the respiration in connection with the temperature factor without any consideration of the species and age peculiarities of the animals. The effect of the temperature upon the live organism is specific and is determined by the qualitative characteristic of the live substrate. The curves of the oxygen consumption by the larvae of individual species under different temperature conditions (fig. 5, 6) are distinguished from each other as per their inclination, length of the rectilinear section, and by the character of the path beyond the limits of this section. We can fully agree with Kozhanchikov (1936, 1936a), Grayevsky (1946) and other authors, who believe that changes in the respiration of insects in relation to the effect of the changing temperature cannot fit at all into any general formula, but that these changes are multiform and reflect in a certain way the qualitative peculiarities of the species.

2. The Gas Exchange Level in Larvae of Different Sizes.

It was noted already long ago, that the intensity of respiration in animals, in the insects in particular, usually increases with the decrease in the body dimensions. One of the expressions of this pattern is the generally known rule of Rubner, according to which the gas exchange in the animals increases in proportion to the increase in their weight to the power 0.67. The constant 0.67 is the power in which the value of the surface changes with the change in the weight, i.e. the cubes of the increase of the surface are proportional to the squares of the increase in weight (volume) of the animals. According to the rule of Rubner the value of the gas exchange in animals of different volume (weight) may be expressed by means of the equation:

$$Y = ap^{k},$$

where _Y_ is the value of the respiration of an animal weighing _p_, _a_ is the value of respiration at p = 1, _K_ is a constant numerically close to 0.67.

Vinberg (1950) found that in general this equation accommodates properly the patterns of changes in respiration intensity in the representatives of the entire class of crustaceans, different in size, and whose fluctuations in weight are approximately as great as one million times. Ivlev (1954) came to a similar conclusion in respect to fishes on the basis of the study of the respiration in many representatives of this class of animals.

Cases are known for insects, when the intensity of their respiration is in direct relation to the weight, to the surface of the body, as well as to the weight and body surface taken together.

Thus, for example, changes in respiration according to formula $y = ap^k$ is recorded for *Locusta* (Butler and Innes, 1936; Simenton, 1933), for drosophilae (Ellenby, 1945), for *Melanopolus* (Bodine, 1921) and for domestic cockroaches (Gunn, 1935).

In other instances the relation may be considerably more complicated. For example, in meal beetle *Tenebrio* the respiration intensity per weight unit decreases with the growth from 5 to 45 milligrams, remains analogous further on, right till the animal reaches a weight of 140 milligrams (Michal, 1931). A similar phenomenon is recorded for *Periplaneta* (Davas and Slater; 1926); when the weight of the cockroach increases from 80 to 200 milligrams, the intensity of the respiration per one unit of weight decreases, with further growth in weight the respiration intensity remains constant. The presence of the mentioned deviations, as well as the considerable fluctuations in constant *k* in the equation $y = ap^k$, makes us question any effort to find a formula, which would accommodate the entire diversity of the relations between the respiration level and the body dimensions in the insects. Finding such a formula would contradict the fact of the difference in the structure of the covers and of their functional possibilities in animals of different species.

We have almost no works on the studies of the level of gas exchange in the chironomid larvae in relation to their dimensions. According to the data of Gorodetsky (1948), the intensity of respiration of Ch. plumosus and Ch. thummi decreases per weight unit with the growth of the animal's length. Sheperklaus (1925) points out that in large Ch. plumosus larvae the oxygen consumption per weight unit is lower than in the small Ch. gregarius larvae. In both cases the authors make no efforts to establish any quantitative relations between the change in the dimensions and the level of respiration. /p. 101

We studied in our article the change in the respiration intensity in the chironomid larvae with their growth, and we have also undertaken a comparison of the gas exchange level in individuals of same size, but belonging to ecologically different species. The measurement of the intensity of respiration in larvae was carried out in a differential respirometer of our own design (Konstantinov, 1956). The readings of the apparatus were taken one hour after the planting of the animals in a manometric flask and continued for a period of 1.5 to 2 hours (every 15 minutes). The obtained results are compiled in tables 33 to 37, in which the oxygen consumption is shown per one larva, as well as per one unit of their weight and of their surface. The latter value is calculated according to the formulae shown in the chapter III (page 197). The indices of the gas exchange intensity shown in tables 33 to 37 are mean values of 6 to 8 measurements, the mean error m usually did not exceed 10 to 12% of M.

The obtained results (tables 33 to 37) speak with certainty of the applicability of Rubner's rule to the chironomid larvae.

With the increase in their weight the consumption in oxygen increases in accordance with the equation $Y = ap^k$, a fact demonstrated most clearly in the rectilinear relation between the gas exchange in the animals and the value of their surface (Fig. 10). The rectilinear equation connecting the gas exchange of larvae to the value of their surface $y = a + bx$, (where y is the respiration value, x is the body surface, and a and b are constants), when applied to different forms, has different initial ordinate and angular coefficient. /p. 102

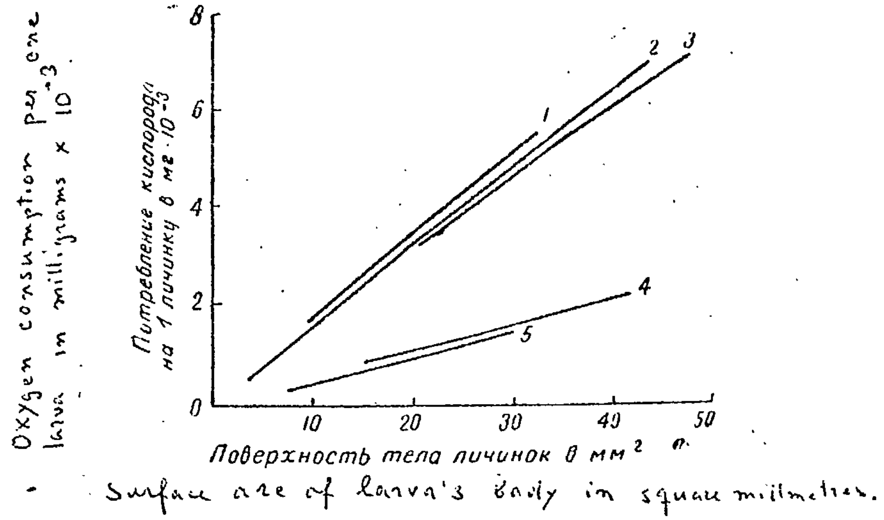


Fig. 10 Oxygen consumption by the Glyptotendipes pallens (1), Chironomus dorsalis (2), Ch. plumosus (3), Syndiamesa nivosa (4) and Prodiamesa olivacea (5) larvae in relation to the increase in their body.

This indicates the fact that although the increase in the gas exchange is in rectilinear relation to the increase in the body surface, the oxygen consumption per surface unit of the covers is, however, not identical in the different forms. In other words, the gas exchange in the chironomids per surface unit does not change with age, but is not identical in individuals of different forms. As we see from tables 33 to 37, the oxygen consumption in milligrams per one square decimeter of the body surface was expressed for various forms by the following mean values: Ch. plumosus: 1.58; Ch. dorsalis: 1.54; G. pallens: 1.68; S. nivosa: 0.53; P. olivacea: 0.50. This difference is, on the one hand, explained by the difference in the thermal conditions under which the respiration of larvae was studied for the individual species. However, also after introduction of thermal corrections according to the equation

$$y_2 = \frac{y_1 \,/1 \neq K(t_2 - 10)/}{1 \neq K(t_1 - 10)}$$

the oxygen consumption per surface unit of the body in the larvae of different species is far from uniform. Thus the oxygen consumption attributed to a temperature at 21^0C (in milligrams per hour) per one square decimetre in Ch. dorsalis larvae is 1.20, in G. pallens larvae it is 1.40, and in P. olivacea larvae it is 0.98.

Table 33.

The oxygen consumption value in Chironomus plumosus larvae of various dimensions (T = 24°C).

1 Вес личинок (в мг)	2 Длина (в мм)	3 Величина поверхности тела (в мм²)	4 Потреблено O₂ (в мг за 1 час)		
			5 одной личинкой	6 на 1 дм² поверхности тела	7 на 1 г сырого веса
3,0	10,0	21,0	32×10^{-4}	1,57	0,96
7,0	13,2	35,0	54×10^{-4}	1,54	0,77
10,0	14,9	47,0	71×10^{-4}	1,52	0,67
23,0	20,6	84,0	131×10^{-4}	1,[illegible]	0,56

Table 34.

The oxygen consumption value in Chironomus dorsalis larvae of various dimensions (T = 27°C).

1. Вес личинок (в мг)	2. Длина (в мм)	3 Величина поверхности тела (в мм²)	4 Потреблено O_2 (в мг за 1 час)		
			5. одной личинкой	на 1 дм² поверхности 6. тела	на 1 г сырого 7. веса
0,2	4,1	3,1	$4{,}7\times10^{-4}$	1,50	2,40
0,5	5,5	5,6	$8{,}5\times10^{-4}$	1,52	1,70
1,0	6,9	9,0	$13{,}4\times10^{-4}$	1,49	1,30
1,1	7,2	10,0	$15{,}0\times10^{-4}$	1,50	1,35
1,7	8,3	14,0	$21{,}7\times10^{-4}$	1,55	1,30
5,0	12,0	27,0	$43{,}0\times10^{-4}$	1,60	0,86
8,8	14,3	39,0	$60{,}5\times10^{-4}$	1,55	0,69
11,0	15,5	44,0	$70{,}0\times10^{-4}$	1,60	0,63

Table 35.

Oxygen consumption value in Glyptotendipes pallens larvae of various dimensions (T = 25°C).

Вес личинок (в мг)	Длина (в мм)	Величина поверхности тела (в мм²)	Потреблено O_2 (в мг за 1 час)		
			одной личинкой	на 1 дм² поверхности тела	на 1 г сырого веса
1,9	6,4	12.0	$19{,}9\times10^{-4}$	1,65	1,04
3,8	8.0	22,0	$37{,}0\times10^{-4}$	1,68	0,98
8,7	10,4	32,0	$55{,}0\times10^{-4}$	1,70	0,63

Table 36.

Oxygen consumption value in Syndiamesa nivosa larvae of various dimensions (T = 11°C).

Вес личинок (в мг)	Длина (в мм)	Величина поверхности тела (в мм²)	Потреблено O_2 (в мг за 1 час)		
			одной личинкой	на 1 дм² поверхности тела	на 1 г сырого веса
2,6	7,7	15,1	$8{,}2\times10^{-4}$	0,54	0,32
3,2	8,2	17,0	$9{,}6\times10^{-4}$	0,53	0,30
5,0	9,6	24 0	$13{,}1\times10^{-4}$	0,55	0,26
12,0	12,8	42,0	$21{,}6\times10^{-4}$	0,50	0,18

Table 37.

Oxygen consumption value in Prodiamesa olivacea larvae of various dimensions (T = 14°C).

Вес личинок (в мг)	Длина (в мм)	Величина поверхности тела (в мм²)	Потреблено O_2 (в мг за 1 час)		
			одной личинкой	на 1 дм² поверхности тела	на 1 г сырого веса
0,7	5,2	7.0	$3{,}2\times10^{-4}$	0,46	0,41
3,0	8,5	19,0	$9{,}6\times10^{-4}$	0,51	0,32
6,0	10,7	30,0	$16{,}8\times10^{-4}$	0,53	0,29

Captions for tables 33 to 37:

1. Weight of larvae (in milligrams)
2. Length (in millimetres)
3. Value of the body surface (in square millimetres)
4. Consumed O_2 (in milligrams per one hour)
5. by one larva
6. per one square decimetre of the body surface
7. per one gram of raw weight.

Therefore, we may assume that the oxygen consumption per one unit of body surface is a good index of the metabolism level in the chironomids and it may be considered as one of the characteristic properties of the species.

It is pointed out in a work of Gorodetskaya (1948), that Ch. thummi larvae, six and ten millimetres long, consumed 435 and 264.7 cubic millimetres of oxygen per one gram of raw weight respectively. Gorodetskaya does not indicate the weight of the assay animals, but according to the equation $P = 3\ l^3$ (see chapter

III) it is 65×10^5 and 3×10^3 milligrams respectively. Consequently, the oxygen consumption per one animal per one hour is in the first /p. 104 case 435 cubic millimetres $\times 65 \times 10^5 = 0.288$ cubic millimetres, and in the second case: 264.7 cubic millimetres $\times 3 \times 10^3 = 0.793$ cubic millimetres.

The surface of the body of assay animals is according to the equation $S = 0.91\, l^2$ (chapter III) is, for larvae six millimetres long, seven square millimetres, and for individuals ten millimetres long, 19 square millimetres. Consequently, the oxygen consumption per one square millimetre of the body surface for the larvae of the smaller size is $\frac{0.283 \text{ cubic millimetres}}{7} = 0.041$ cubic millimetres, for the larger ones: $\frac{0.793 \text{ cub. mm.}}{19} = 0.042$ cubic millimetres.

This similarity in the obtained figures confirms once more our conclusions that the oxygen consumption ascribed to the value of the surface of a larvae does not change with the growth of the animal.

3. Relation between the Gas Exchange in Larvae and the Partial Pressure of Oxygen

Regardless of the considerable practical importance of correct understanding of the effect that the partial pressure of oxygen has upon the gas exchange in the chironomid larvae, the available published data on this subject are obviously insufficient and contradictory to a considerable degree. According to Garnish (1936) the gas exchange in the Ch. thummi larvae is only very slightly dependent on the pressure of oxygen and only when the latter drops below 3% of the atmospheric pressure, the intensity of the respiration of the animals begins to decrease. Ever (1942) obtained different results for the ecologically similar Ch. plumosus. In his experiments the gas exchange of the animals remained invariably in direct relation to the oxygen pressure for all the tested concentrations of the gas (0.5 to 6.5 milligrams per litre, or approximately 1 to 13% of the atmospheric pressure). According to Walsh's data (1948) the intensity of the respiration of the T. brunnipes and A. nebulosa larvae begins to decrease with the decrease in the oxygen concentration below 6.5 milligrams per litre. In the case of Ch. longistylus and A. varia larvae the decrease in the respiration intensity is only observed when the oxygen concentration decreases below 3.5 milligrams per litre (Walsh, 1948).

The results of our studies on the relation between the gas exchange in larvae and the partial pressure are reflected in table 38. The data shown in this table on individual measurements represent a mean value of 15 to 20 measurements obtained by the flask method. The mean error m, as a rule, constituted from 6 to 8% of M.

It is easy to see that in all the instances studied by us (table 38), we can perfectly clearly trace the relation between /p. 105 the respiration values in the larvae and the oxygen pressure within the range of all the gas concentrations that may normally occur in water. Therefore the very responsible conclusion of Garnish (1936) on the independence of the gas exchange in the larvae and the oxygen concentration, when the latter's pressure exceeds 3% of the atmospheric pressure, should be considered erroneous. Just as erroneous is the concept of Garnish (1930) of a certain "stability" in the level of respiration in the chironomid larvae caused by some special control mechanisms.

Table 38.

Intensity of gas exchange in certain chironomid larvae in relation to the oxygen concentration (in milligrams of O_2 per one gram of raw weight per one hour).

Ch. plumosus		Ch. dorsalis		Glyptotendipes pallens		Syndiamesa nivosa		Prodiamesa olivacea	
концентрация O_2 (в мг/л) 1	интенсивность газообмена 2	концентрация O_2 (в мг/л) 1	интенсивность газообмена 2	концентрация O_2 (в мг/л) 1	интенсивность газообмена 2	концентрация O_2 (в мг/л) 1	интенсивность газообмена 2	концентрация O_2 (в мг/л) 1	интенсивность газообмена 2
0,3	0,14	0,6	0,18	0,4	0,16	0,5	0,04	0,8	0,05
0,6	0,19	1,2	0,26	0,7	0,21	1,4	0,07	1,6	0,10
1,6	0,36	2,2	0,32	1,2	0.26	3,5	0,14	2,8	0,14
3,6	0,43	4,8	0,38	5,2	0.63	8,9	0,26	8,5	0,28
7,1	0,55	9.3	0,60	7,5	0,68	12,7	0.34	12,3	0,37

Captions in the table:

1. concentration of O_2 (in milligrams per litre)
2. intensity of gas exchange.

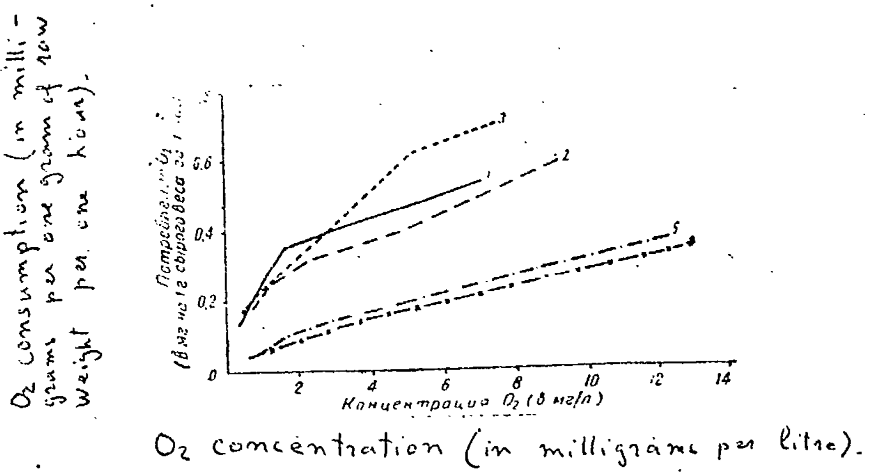


Fig. 11. The oxygen consumption by the larvae Chironomus plumosus (1), Ch. dorsalis (2), Glyptotendipes pallens (3), Syndiomesa nivosa (4) and Prodiamesa olivacea (5) in relation to the oxygen content in water.

We may assume, that there are principal differences in the respiration of forms containing hemoglobin (Ch. plumosus, Ch. dorsalis, /p. 106 G. pallens) and of those devoid of it (S. nivosa, P. olivacea). In the first ones the curves of the oxygen consumption (fig. 11) under conditions of the changing pressure have a less rectilinear character, than the second ones have, particularly in the diapason of the low oxygen pressures. The respiration intensity in forms with hemoglobin, when the oxygen concentration decreases from 3 to 0.3 - 0.6 milligram per litre, decreases by 2 to 2.5 times, but in larvae devoid of hemoglobin the gas exchange, under equal conditions, decreases by 3 to 5 times.

It is interesting to note, that analogous differences in the gas exchange, but pronounced with a still greater sharpness, are observed in larvae with functioning and with excluded (by means of CO) hemoglobin (Ever, 1942; Walsh, 1946b). This gives us a basis to express the hypothesis concerning the presence in the larvae with hemoglobin of two transportation paths of oxygen: by means of the pigment and without the latter. The existence of the first form of respiration is proved by the fact of the decrease in the gas exchange in animals under water with low oxygen content in the case of hemoglobin exclusion (Garnish, 1936; Ever, 1942; Walsh, 1947). The possibility of oxygen transportation without any participation of hemoglobin appears from experiments of Garnish (1936), Ever (1942) and Walsh (1947). In their experiments the larvae of the genera Chironomus and Tanytarsus, kept in well aerated water, did not change the level of the gas exchange after the exclusion of hemoglobin.

The presence of two respiration mechanisms: the diffusion mechanism and the one operating by means of the pigment, creates the difference in the gas exchange of the larvae, both of those that have hemoglobin, and of those devoid of it. Evidently, the transportation of oxygen by the way of diffusion must be inhibited in proportion to the drop in the gas pressure in the surrounding medium, the transfer of oxygen, on the other hand, by means of pigment depends on the concentration of gas to a much lesser degree.

Therefore, the forms with excluded hemoglobin have a respiration intensity, which differs sharper and sharper from the respiration intensity in animals with functioning pigment, when the oxygen concentration decreases. When comparing our data with the observation results of Ever (1942) and Walsh (1947c), we may come to the conclusion that in forms without hemoglobin the respiration inhibition with the decrease in the gas concentration is not as sharply pronounced, as in larvae with excluded hemoglobin, but stronger, than in animals with functioning pigment. We may assume on the basis of the said, that forms devoid of hemoglobin obtain their oxygen not only by means of diffusion, but have some form of additional respiratory mechanism, which functions the most efficiently (although somewhat less efficiently than the hemoglobin) at low oxygen pressures. /p. 107

In a number of works Garnish (1953a, b, d; 1954a; 1955a, e; 1956; 1956d) traced in the chironomid larvae characteristic changes in the tracheal system consisting in a widening of stems, when the surrounding medium became respiratorily unfavourable.

It is most probable that an expansion in the lumens within the tubes of the tracheal system increases the possibility of gas diffusion and is an additional device for supporting the gas exchange under conditions of oxygen deficit. Let us remember that in forms devoid of hemoglobin the tracheal system is, as a rule, developed considerably stronger than in red larvae. However, in all cases it is covered and hardly possesses any considerable functional possibility. Therefore, it is quite appropriate to assume that in forms devoid of hemoglobin, there is some other respiratory pigment, which assists the larvae in gas exchange in a respiratorily unfavourable medium.

To evaluate correctly the functional role played by hemoglobin, it is extremely important to determine the diapason of the oxygen pressures, within which the pigment may serve as gas carrier.

According to Leich (1916) complete satiation of hemoglobin with oxygen in the larvae of the *Chironomus* genus only occurs, when the gas pressure equals 7 millimetres of mercury column, i.e. is approximately 0.8% of the atmospheric pressure (4% of the water saturation). When the pressure drops down to 5.0 and 2.9 millimetres of mercury column the satiation of the hemoglobin decreases correspondingly to 60% and to 16.5% (the temperature being 17°C). Such a steep character of hemoglobin dissociation curve in the chironomids confirms also the data of Fox (1945). In his experiments the hemoglobin of the *Ch. riparius* larvae had a 50% satiation, when the oxygen pressure attained 0.5 millimetres of mercury (temperature being 10°C).

On the basis of the data on the complete satiation with hemoglobin of chironomids in the presence of very small concentrations of oxygen, Leich (1916), Pause (1918) and Garnish (1936) assume that the pigment cannot function in the larvae, which are in aerated water, because the pigment will always exist in the form of oxyhemoglobin, i.e. it will not serve alternatively now as acceptor, and now as a donor of the respiratory substrate. Such a conclusion is completely wrong, because it is based on the identification of the external medium with the interior one, although, in reality the pressure of oxygen in the animal's lumen-fluid is always considerably lower, than outside of the limits of their body. For example, in the earthworms the oxygen pressure in the lumenal liquid is 14 millimetres of the mercury column, when the gas pressure in the surrounding medium attains 160 millimetres (Adler, 1917). In the case of the chironomids there are no direct data on the oxygen pressure in the tissues, but one may assume, that it is very small. According to the data of Aleksandrov (1934) and Sinitsa (1937), the oxidation-reduction potential in the tissues of the silty chironomids is very low (rH = 5-7) and, apparently, the oxygen pressure in the lumenal liquids of the animals was several times smaller, than in the surrounding medium. Therefore, even in a case of a comparatively high content of oxygen in the water, its pressure in the chironomid tissues may be so low, that the hemoglobin will transform from the oxidized form, to the reduced one, i.e. it will preserve its functional value.

On the basis of the obtained material (table 38), we believe contrary to the opinion of Garnish (1936), Ever (1942) and

Walsh (1947b), that the upper limit of the oxygen concentration, at which the hemoglobin participates in its transportation, is not less than 5 to 6 milligrams per litre. This conclusion is actually supported by factual data presented by Walsh (1947), when she determined the simultaneous presence in the blood of Ch. plumosus of hemoglobin and oxyhemoglobin at all the oxygen concentrations up to 100%-satiated water. The conclusion concerning the participation of hemoglobin of the larvae in the oxygen transportation within an extensive diapason of the pressure of this gas, finds a certain support also in the published data on the respiration of forms living under approximately identical conditions, as the chironomids do. Johnson (1941) points out, that contrary to the old concepts, there is not a single animal species for which the fact of the elimination of the hemoglobin function in the presence of high oxygen concentrations could be extablished. On the contrary, the participation of the pigment in the transportation of oxygen, when its pressure in the surrounding medium is equal to the atmospheric pressure, is recorded by Johnson (1941), Dausend (1931), Jürgens (1935) and by Krüger (1938) for the earthworms, for the Tubifex oligochaeta and for Nereis polychaeta.