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THE MAIN PARAMETERS REGULATING THE LEVEL OF ENERGY EXPENDITURE IN AQUATIC ANIMALS

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ABSTRACT

The cost of maintenance in energy balances of some animal species is presented. Widely used methods for the determination of oxygen consumption are characterized on the basis of their errors. Some factors modifying the intensity of oxygen consumption are discussed: body size, developmental stage, the quantity and quality of food, the availability of oxygen and also the importance of respiratory movements of *Perlodes intricata* (Plecoptera) larvae in different temperature-oxygen combinations.

INTRODUCTION

An energy balance can be expressed by the equation: $C = P+M+F$. From these, only one element, metabolism (M) will be discussed here. Most attention will be paid to oxygen consumption, carbon dioxide production and to the energetic significance of these processes.

In the biological literature may be found many records of rates of oxygen consumption for different species of animals. As is known, these results are often relevant only for the actual conditions of the experiment, as respiratory rate is regulated by many factors, such as body size, developmental stage, food, availability of oxygen and others. A full presentation of these problems is not possible here and examples of respiratory results have been confined to those measured in the Department of Experimental Hydrobiology, Nencki Institute of Experimental Biology, Warsaw, Poland. Not only aquatic species are considered, some terrestrial animals are also included. Much of the work presented here is very recent, some is still unpublished and I am greatly indebted to my Colleagues for allowing me to use their results.

As is known, energy such as faeces (F) leaving an organism remains in the ecosystem and may be subsequently utilized by another trophic level. Energy expended for metabolism however is irretrievably lost from the whole ecosystem. The cost of maintenance is an important part of a species' energy balance. As can be seen from Fig. 1, the cost of maintenance cumulated for the whole larval development of *Lestes sponsa* (Odonata) represented 36% of assimilated energy (FISCHER 1967). Analogous data for five other animal species are presented in Table I. The cumulated cost of maintenance can be as much as 79% of assimilated energy (*Tribolium castaneum*, reproducing adults excluded; KLEKOWSKI et al. 1967).

Table I. Cumulated maintenance energy as per cent of cumulated assimilated energy

Species	$\frac{M_c}{A_c}$ %	For period of life cycle cumulated	Author
Lestes sponsa (Odonata)	36	whole larval life	FISCHER (1967)
Simocephalus vetulus (Cladocera)	37	first 20 days of life (12 days of reproductive life)	KLEKOWSKI and IVANOWA (unpublished)
Asellus aquaticus (Isopoda)	45	first 116 days of life	PRUS (unpublished)
Macrocyclops albidus (Copepoda)	50	copepodites	KLEKOWSKI and SHUSHKINA (1966)
Tribolium castaneum (Coleoptera)	79	first 36 days of life	KLEKOWSKI et al. (1967)

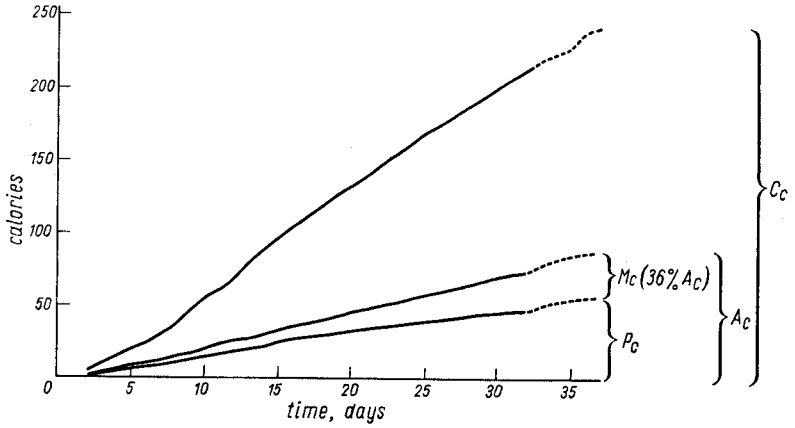

Fig. 1. Cumulative energy budget of an average larva of *Lestes sponsa* (adapted from FISCHER 1967). C_c — cumulated food intake, A_c — cumulated assimilation, M_c — cumulated cost of maintenance, P_c — cumulated production

METHODS

We can see clearly from above, that it is worth determining exactly the value of metabolism. Therefore, errors due to the method of measurement should be de-limited at the beginning. Methods which are commonly used for the measurement of respiration of aquatic animals can be roughly classified into two groups. The first are gasometric methods; the oxygen consumption itself occurs in the liquid phase, but changes in the amount of oxygen are measured in the gaseous phase. The second group are the methods where both the measured processes as well as its measurement occur in the aqueous phase.

It is assumed, that in the gasometric methods both phases, aqueous and gaseous, are in ideal equilibrium. Presumably this is not always realized, considering that the rate of diffusion of oxygen in water is about 3 millions less than in air. WINBERG et al. (1963) have proved, that poor diffusion of

oxygen from air into water in a gasometric respirometer can be a cause of false results of oxygen consumption when sluggish animals are investigated. That is why for aquatic animals one has to avoid the use of gasometric methods. However, micro-gasometric methods such as the cartesian diver method, are at present the only adequate method for respiration measurements of very small animals such as Protozoa, Rotatoria and small Cladocera.

From among the methods of measurement of respiration in aqueous phase, two techniques have been most frequently used; one is the closed-bottle method and another the flowing-water method. The closed-bottle method is simple, however its results are charged with serious errors when the method is applied in its "classic" way, i.e. when the bottle is closed immediately after the animals have been placed inside and when the changes in the oxygen concentrations before and after an exposition period are

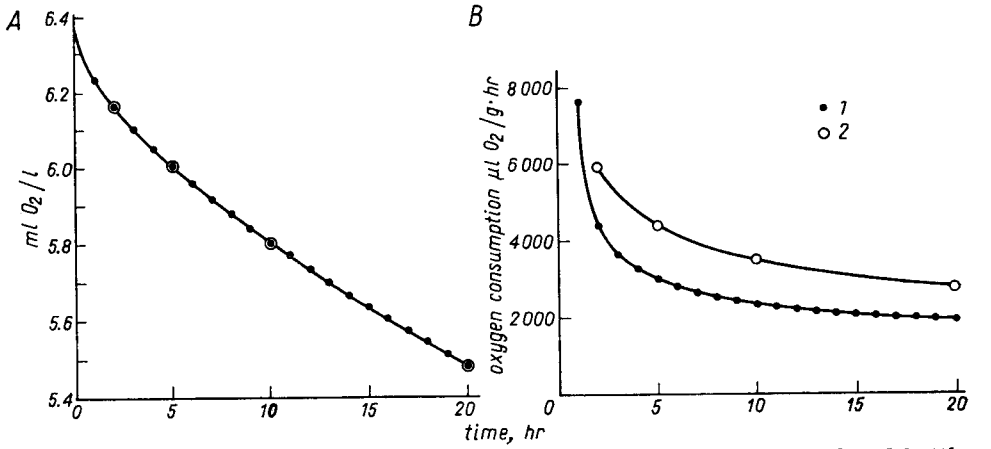

Fig. 2. Theoretical example of oxygen consumption measured by the closed-bottle method (from KAMLER 1969). *A* — changes in the oxygen concentration in the bottles containing animals: 1 — hourly electrode readings, 2 — WINKLER results (after 2, 5, 10 and 20 hours). *B* — oxygen consumption by animals: 1 — real oxygen consumption, calculated from the electrode readings, 2 — apparent oxygen consumption, calculated from WINKLER results

used as a basis for the oxygen consumption calculation. Many authors (HARNISCH 1938, ZEISS 1963, KAMLJUK 1964, PATTÉE 1965, MANN 1965) point out, that an animal directly after being placed in an experimental vessel shows heightened activity and intense respiration followed by a period of lowered and more uniform oxygen consumption. This problem is illustrated by a theoretical example (KAMLER 1969) in Fig. 2. The curve 2A represents the actual dissolved oxygen concentrations in four bottles containing animals closed for periods 2, 5, 10 and 20 hours. The dissolved oxygen concentrations in these bottles were recorded at hourly intervals by oxygen electrodes (points in graph) but only at beginning and at the end of the exposition period by the Winkler chemical method (open circles in graph). Curve 1 in Fig. 2B represents the rate of oxygen consumption calculated from the curve 2A, from the oxygen concentrations at the beginning and at the end of each hour (electrode determinations). On the other hand, the curve 2 on Fig. 2B represents the rate of oxygen consumption calculated from the same curve 2A, but

from the oxygen concentrations at the beginning and at the end of each exposition period (Winkler determinations). As can be seen from a comparison of curves 1 and 2, the rates of oxygen consumption for the same animals in the same bottles are very different and the question is which to accept as realistic. It seems, that curve 1 is closer to the real oxygen consumption rates, as it shows high values at the beginning and more uniform values at the longer exposition times. Curve 2, however, gives consistently higher rates probably because it includes the initial period of heightened metabolism; the longer the exposition time, the less is the difference between these two curves. KAMLER (1969) compared the respiratory rates of three freshwater species, using closed-bottle-Winkler method and flowing-water polarographic

Table II. Oxygen consumption measured simultaneously by two methods. Exposition time 0–50hr. (KAMLER 1969)

Species	Oxygen consumption, $\mu l\, O_2$ g dry wt · hr			t°C ∓0.015	Mean dry weight, mg ∓ std. error
	closed-bottles + Winkler (t=time, hr)	flowing-water respirometer + electrode			
		mean ∓ std. error	std. error, %		
Cloeon dipterum (Ephemeroptera)	$7500 \cdot t^{-0.336}$ $N = 27$	1859∓60.1 N=33	3.2	20	0.214 ∓0.0045
		2655∓87.9 $N = 27$	3.3		
Isoperla buresi (Plecoptera)	$1750 \cdot t^{-0.377}$ $N = 8$	282.8∓10.77 $N = 5$	3.8	8	5.34 ∓0.374
*Bithynia tentaculata** (Gastropoda)	$192 \cdot t^{-0.459}$ $N = 24$	74.7∓2.62 $N = 27$	3.5	20	52.2** ∓3.64

N = Number of measurements.
* Measured in collaboration with A. F. ALIMOV, Leningrad.
** Weight of body with shell.

method simultaneously (Table II). The results obtained with the closed-bottle method were lower with longer exposition times, as in curve 2 Fig. 2B. The scatter in the results was great and, particularly when the exposition time was short, maximal values could be five times greater than the minimal ones. The results of the flowing-water method, on the other hand did not differ with time of exposition even up to 50hr; moreover the scatter of the results was very small. FISCHER (unpublished) measured the respiration of *Ctenopharyngodon idella* (Pisces) in another type of flowing-water respirometer; the standard error of her results was 3.5% of the mean, which is very similar to the data presented on the Table II. Similarly, WINBERG et al. (1963) observed, that the oxygen consumption of *Bithynia tentaculata* and two other *Gastropoda* species measured during 24hr in a flowing-water respirometer, oscillated about a mean, but without any regular changes. These authors, as well as the author of present paper, consider that compared with closed-bottle methods, the flowing-water methods provide more realistic information about the respiration of aquatic animals. Therefore, the flowing-water methods are

to be recommended; unfortunately, when the respiratory rate of a single individual weighing less than 1.5 g of live weight has to be measured, the water outflow from the respirometer should be small, about 200 ml/hr or less so that it is no longer possible to determine the oxygen concentration by the Winkler method and a polarographic method must be used. A flowing-water polarographic respirometer (KLEKOWSKI and KAMLER 1968) is presented on the Fig. 3. An animal is placed in the respiration chamber which is immersed

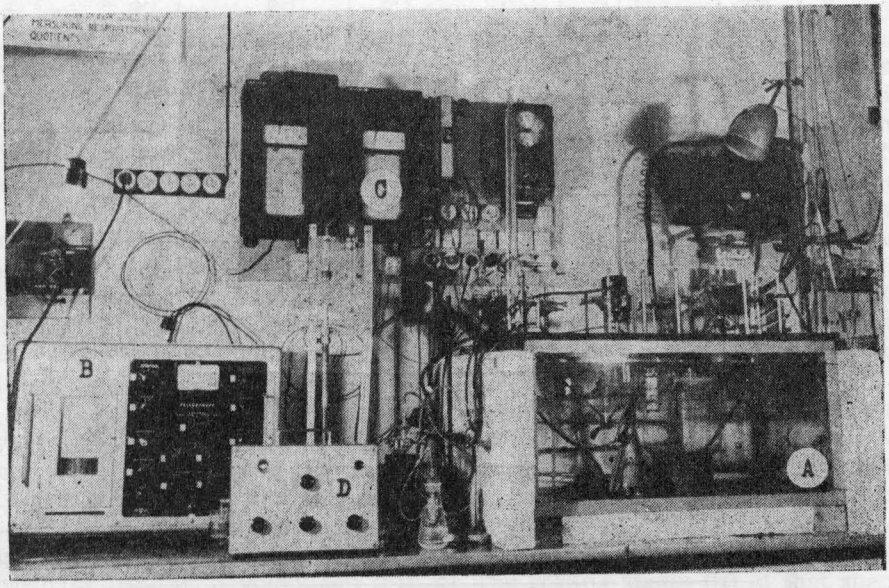

Fig. 3. General view of the flowing-water polarographic respirometer (from KLEKOWSKI and KAMLER 1968). A — constant temperature bath with reservoir-bottles, respiration chamber and electrode chamber, B — polarograph, C — temperature recorder, D — conductivity metre

in the water-bath (A). The water flow, the temperature and the level of oxygen in the inflowing water are stable and controlled. The oxygen recorder (B), the temperature recorder (C) and the conductivity meter (D) can be also seen.

RESULTS

As is known, the relationship between oxygen consumption and body weight in animals belonging to the same species can be described by the formula $QO_2 = a \cdot W^b$, where a is the oxygen consumption per 1 hour of an individual whose weight equals unity, b shows the degree of dependence of metabolic intensity upon the weight. The values of b are the most frequently from 0.67 (surface) to 1.00 (weight) and are disposed around 0.75 (HEMMINGSEN 1960). Many factors can influence a and b, for instance the type of body construction, intensity of growth, temperature, food availability and many others. The experimental results, obtained in our laboratory, are presented in

Table III. Oxygen consumption related to body weight

Species	Experimental data		O_2 consumption of 1 individ. weighing 1 mg converted to 20°C, µl/hr	live weight, mg	for period	Authors
	O_2 consumption µl/ind. · hr (W = live wt., mg)	temp. °C				
1. *Macrocyclops albidus* (Copepoda)	$0.404 \cdot W^{0.840}$	21	0.372	0.001—0.040	whole life	KLEKOWSKI and SHUSHKINA (1966)
2. *Rhizoglyphus echinopus* (Acarina)	$0.711 \cdot W^{0.830}$	24	0.510	0.001—0.050	whole life	STĘPIEŃ (unpublished)
3. *Simocephalus vetulus* (Cladocera)	$0.605 \cdot W^{0.874}$	22	0.512	0.017—0.350	whole life	KLEKOWSKI and IVANOVA (unpublished)
4. *Tribolium castaneum* (Coleoptera)	$19.900 \cdot W^{0.850}$	29	9.572	0.02—3.50	all feeding larval stages	KLEKOWSKI et al. (1967)
5. *Asellus aquaticus* (Isopoda)	$0.285 \cdot W^{1.000}$	23	0.222	5—30	first 100 days of life	PRUS (unpublished)
6. *Polydesmus complanatus* (Diplopoda)	$1.080 \cdot W^{0.680}$	23	0.841	5—90	second half of larval life + adult life	STACHURSKA (unpublished)
7. *Perlodes intricata* (Plecoptera)	$0.631 \cdot W^{0.659}$	10,5	1.600	90—200	second half of larval life	KAMLER (unpublished)
8. *Ctenopharyngodon idella* (Pisces)	$8.002 \cdot W^{0.598}$	23	6.234	20,000—50,000	first year of life (whole life about 6 years)	FISCHER (unpublished)

Table III. They have been converted to common units: QO_2 is expressed in μl O_2/ind.·hr, W in mg of live weight. The oxygen consumption of a hypothetical individual weighing 1 mg have been converted to temperature of 20°C in way proposed by WINBERG (1956). This is high in Tribolium (9.572 μl O_2/hr) and in Ctenopharyngodon (6.234 μl O_2/hr) probably because of the fact, that both species were reared in excess of food. Moreover, the Tribolium equation is calculated for larval 2nd–6th (7th) instars whose respiratory rate is high. The respiration of younger and older stages of Tribolium is much more low. The intensity of oxygen consumption in Perlodes (1.600 μl O_2/hr) is much lower than in Tribolium and Ctenopharyngodon but fairly high in comparison with the remaining species. ISTENIČ (1963) measured the oxygen consumption of another ecologically and physiologically similar stonefly species, *Perla marginata*, in individuals weighing between 3 to 460 mg. She obtained 0.784 μl O_2/hr for one individual weighing 1 mg in 15°C or 1.231 μl O_2/hr after conversion to 20°C, which is close to that obtained by KAMLER (unpublished) for Perlodes, 1.600 μl O_2/hr. A high oxygen consumption intensity is easily understood in animals which, like Plecoptera, live in low temperature conditions. The experimental temperatures, 10.5°C for Perlodes and 15°C for Perla are close to upper limit of their natural temperature ranges. ISTENIČ (1963) also records a "b" value of 0.668 for Perla, which is also close to 0.659 for Perlodes (Table III). The investigations on Asellus, Perlodes and Ctenopharyngodon are still in progress.

As an organism grows and develops, not only its body size can influence the oxygen consumption, but in many cases the oxygen consumption can increase allometrically. Frequently older forms have a lower metabolism than intensively growing young forms. However the periods of more and less intense metabolism appear in different parts of life cycle in different species. STĘPIEŃ (unpublished) measured the oxygen consumption of *Rhizoglyphus echinopus* (Acarina) during its development (Fig. 4). The resting stages (R) in that species alternate with the active stages (A). As can be seen from Fig. 4, the increment of the oxygen consumption of the resting stages is less than that of the active stages.

Data from KLEKOWSKI and SHUSHKINA (1966) on the respiration of *Macrocyclops albidus* are presented in Table III. The regression coefficient b was 0.84. This value was obtained when the results for nauplii, copepodites and adults were taken together. However, if these developmental stages are considered separately, it will be found, that the regression coefficient b will be 0.34 for nauplii, whereas it will be 1.02 for older developmental stages. Furthermore, animals were cultured in different food concentrations and again there was a respiratory difference between nauplii and the older stages; the increase in oxygen consumption per weight increment was less in the nauplii than in the older stages ($b = 0.27$ for nauplii compared with $b = 0.78$ for older stages and, similarly for another food concentration, $b = 0.45$ and $b = 1.04$).

Information on the influence of quantity of food on metabolism are included in the work of STACHURSKA (unpublished). She measured the oxygen consumption of carnivorous protozoan, *Dileptus cygnus*, which was fed with different concentrations of Colpidium. When the density of the prey was ten and five times greater than that of the predator, the predator's respiratory rate was 35.5 cal·10^{-5}/ind.·24hr, however, at density ratios of 3 : 1 and 1 : 1, the respiratory rate decreased to 13.4 and 8.06 cal·10^{-5}/ind.·24hr respectively.

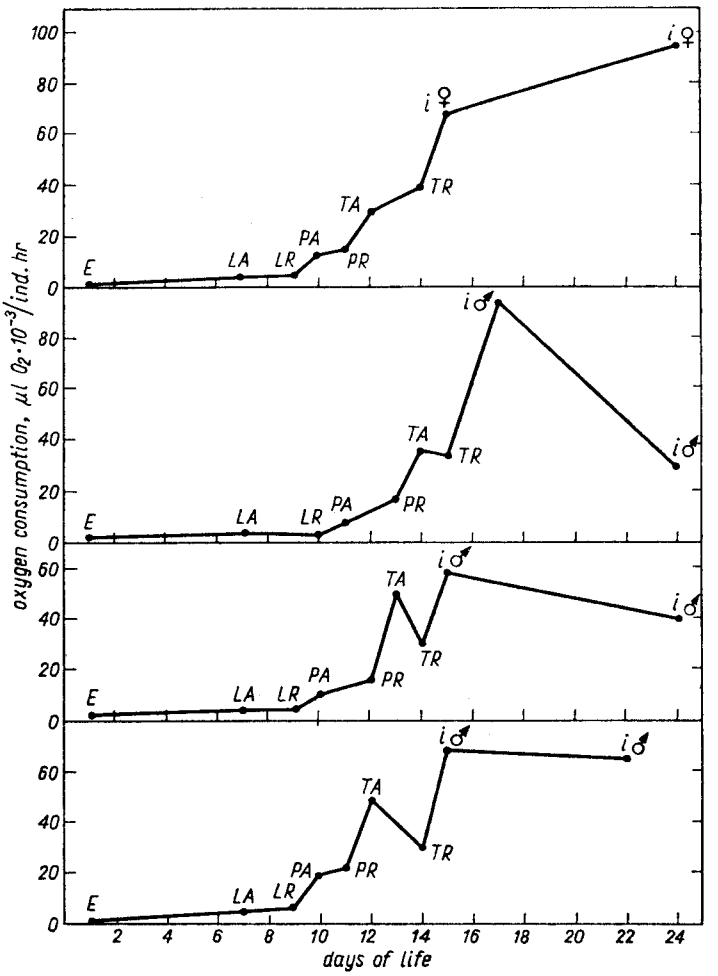

Fig. 4. Oxygen consumption of *Rhizoglyphus echinopus* during development (adapted from Stępień, unpublished). E — egg, L — larva, P — protonympha, T — tritonympha, I — imago, A — active stages, R — resting stages

Further information about the influence of quantity of food on metabolism are presented in the previously mentioned paper of Klekowski and Shushkina (1966). The oxygen consumption of *Macrocyclops albidus* in different concentrations of the food species, *Paramecium aurelia*, is presented in Fig. 5. When food is supplied in low quantities, 1000 protozoans/l, metabolism of the predator is the lowest in all classes of body size — curve I. The characters of metabolism curves are similar in food concentrations of 10,000 and 50,000 protozoans/l and show an uniform increase in metabolism with size — curves II and III. When food was supplied in abundance, 100,000 protozoans/l, increase in body weight of Macrocyclops up to about 10 µg is accompanied by intense increase of metabolism, but further increases of body weight produce less intense changes in metabolism — curve IV. The authors interpret the latter phenomenon as lowered activity in better fed animals.

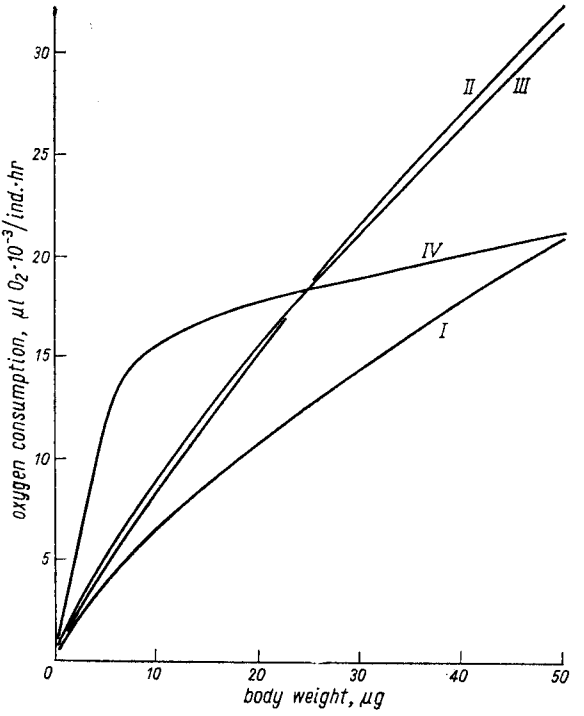

Fig. 5. Relationship between oxygen consumption and weight of *Macrocyclops albidus* in different food concentrations (from KLEKOWSKI and SHUSHKINA 1966). I — 1000 ind./l, II — 10,000 ind./l, III — 50,000 ind./l, IV — 100,000 ind./l.

The rate of energy use by an animal is influenced not only by the abundance of food, but also by its composition. It is known, that the calorific value of 1 µl of consumed oxygen changes according to what kind of substance is metabolized. Three ways of estimating the energy used are presented in Table IV. Each calculation takes account, but to a different degree, the types of substances being metabolized. In the first calculation, only the measured oxygen consumption is considered, but is converted into calories by means of an oxy-calorific coefficient which is assumed to be the same value in all determinations. The amount of metabolized energy obtained in this calculation is defined as 100%. In the second type of calculation, both the oxygen consumed and carbon dioxide produced are considered; the basic assumption in this calculation is that only carbohydrate and fat substances are being metabolized. Having obtained a respiratory quotient (*RQ*) the oxy-calorific coefficient characteristic for this *RQ* may be taken from tables, e.g. in HARROW and MAZUR (1958). The third calculation takes into account the results of determination of oxygen consumed, carbon dioxide produced and nitrogen excreted. The rates of energy utilization, calculated in these three ways, differ only slightly from each other, the differences are less than 2%. But, as can be seen from Table IV, the full determination of all three parameters, oxygen consumption, carbon dioxide production and nitrogen excrection, allows the quantitative estimation of the participation of metabolized carbohydrates, fats and proteins. BŁAŻKA (1966) showed that the participa-

Table IV. Three ways of estimation of metabolism

Determined	Species / based on results of		*Ctenopharyngodon idella* (Pisces)		*Tribolium castaneum* (Coleoptera)	
			Fischer (unpublished)		Prus (1968)	
			fish 52g	average fish	larval V instar	adult male
I O_2 cons.	O_2 cons., μl/ind. · hr		4629.04	4557.00	4.1507	5.9527
	oxy-calorific coeff., cal/μl O_2		$4.84 \cdot 10^{-3}$			
	energy metabolized cal/ind. · hr		22.405 (100.00%)	22.056 (100.00%)	0.02009 (100.00%)	0.02881 (100.00%)
II O_2 cons. CO_2 prod.	CO_2 prod., μl/ind. · hr		4066.40	4123.00	3.6526	4.7622
	RQ general		0.88	0.90	0.88	0.80
	oxy-calorific coeff., cal/μl O_2		$4.899 \cdot 10^{-3}$	$4.924 \cdot 10^{-3}$	$4.899 \cdot 10^{-3}$	$4.801 \cdot 10^{-3}$
	energy metabolized cal/ind. · hr		22.678 (101.21%)	22.439 (101.74%)	0.02033 (101.19%)	0.02858 (99.19%)
III O_2 cons. CO_2 prod. N prod.	N prod. μg/ind. · hr		227.24	232.40		
	RQ nonprotein		0.91	0.95		
	energy metabolized cal/ind. · hr	carbohydr.	11.436	13.379		
		fat	5.013	2.727		
		protein	6.107	6.245		
		total	22.556 (100.67%)	22.351 (101.34%)		

tion of protein metabolism in *Daphnia hyalina* can be as high as 80% of whole metabolism. The utilization of proteins as a fuel increased as the food supply decreased. BLAŻKA suggests that as more protein is metabolized, less is available for tissue production, so that the time development of the animals becomes longer. The amount of metabolized protein is calculated directly from the measured values of nitrogen excrected. However, quantitative interpretation of the participation of metabolized carbohydrates and fats needs care. It is based upon a non-protein respiratory quotient: $RQ = 1$ for carbohydrates and $RQ = 0.7$ for fats. But other processes, beside combustion,

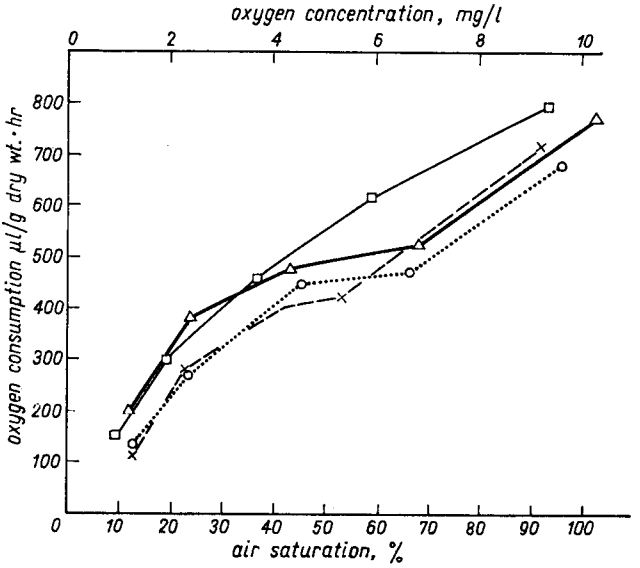

Fig. 6. Oxygen consumption of four *Anax imperator* larvae in relation to the oxygen content in water (from KLEKOWSKI and KAMLER 1968)

can also modify RQ and can cause lower or higher RQ than the limits mentioned above. For example, one situation when RQ can be higher than 1 is the conversion of carbohydrates into fats.

As is known, the problem of availability of oxygen is of special importance for aquatic animals, because the oxygen concentration differs greatly from air saturation in some periods or places of aquatic milieu. Animals may regulate their oxygen consumption in high oxygen concentrations; the oxygen consumption is then independent of oxygen concentration. When the oxygen content of milieu decreases down to some critical pressure, the oxygen consumption of animals declines rapidly with further decrease of oxygen concentration. Critical pressures of oxygen differ greatly in different animal species. Many species (conformers) even at air saturation do not fully reveal their potential use of oxygen. The oxygen consumption of a single *Anax imperator* larva was measured in five oxygen concentrations, Fig. 6 (KLEKOWSKI and KAMLER 1968). The flowing-water polarographic respirometer, described above, was used. The dependence of respiration on the oxygen content is visible in all oxygen concentrations. Below 23% of air saturation the oxygen consumption rate decreases more markedly.

Different kinds of adaptations permit the regulation of metabolism in reduced environmental oxygen. An important adaptation are the respiratory movements of different types. These respiratory movements reduce the boundary layers at respiratory surfaces, and, so diminish the oxygen gradients. *Perlodes intricata* larvae exhibit such respiratory movements; the body undulates vertically. The frequency of the movements per unit time is of special

Table V. Plan of the experiment on respiratory movements of *Perlodes intricata* larvae; (habitat: mountain streams, extremal temperatures 1.5–14°C). Ten animals were measured separately in each temperature-oxygen combination

Temp.°C	Oxygen content in per cent of air saturation (total number of 1-min readings in brackets)				
5.5	26.0 (10)*	47.1 (159)	69.1 (257)	113.2 (278)	194.0 (576)
10.5	33.6 (23)	42.5 (39)	76.1 (105)	108.3 (190)	133.5 (201)
15.5	25.8 (10)*	57.2 (32)	79.9 (55)	106.5 (92)	123.1 (128)

* means the death of all ten animals before the first reading.

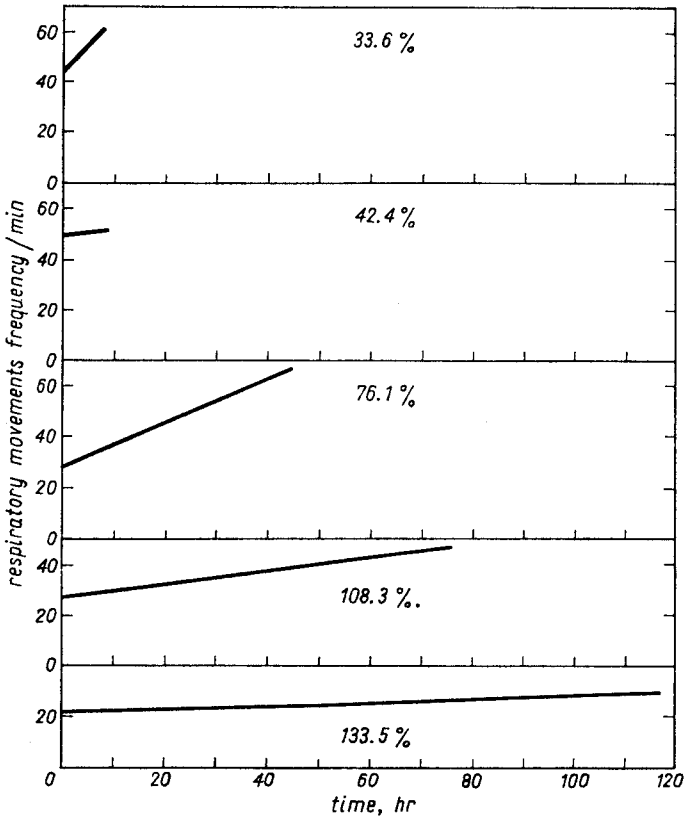

Fig. 7. Relationship between O_2 concentration and frequency of respiratory movements in *Perlodes intricata* larvae at 10.5°C (from KAMLER, unpublished). Per cent of air saturation at the start of experiment is indicated

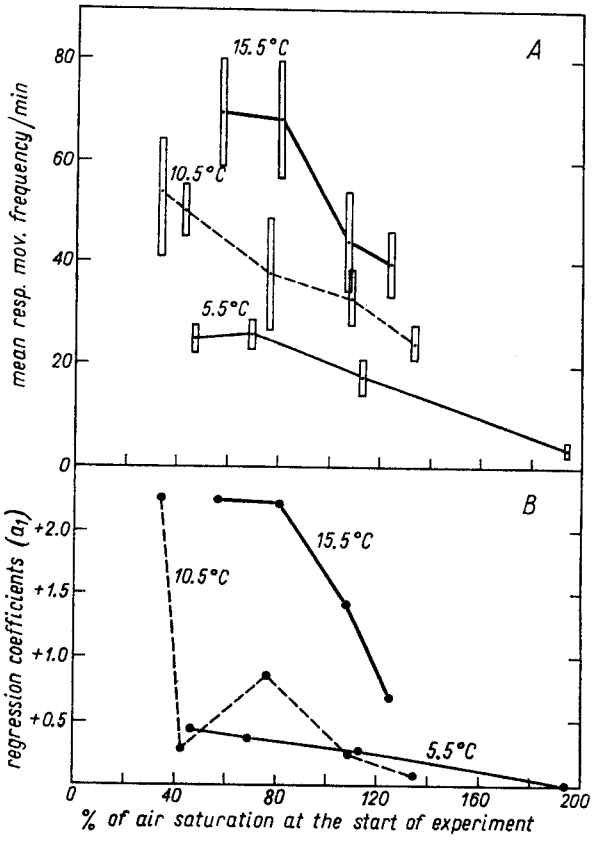

Fig. 8. Respiratory movement frequency in *Perlodes intricata* larvae in different combinations of oxygen and temperature (from KAMLER, unpublished). A — mean respiratory movement frequency/min. Vertical rectangles show 95% confidence interval, B — regression coefficients (a_1) of respiratory movements (y) on time (x), from the formula $y = a_0 + a_1 \cdot x$

interest. KAMLER (unpublished) carried out 3 series of experiments; the aim of them was to determine how temperature and oxygen concentration influence the frequency of respiratory movements.

Single animals were enclosed in 150 ml bottles with water and the frequency of their respiratory movements per minute was recorder at regular intervals up to their death. This was carried out at three temperature and for each temperature, five different concentrations of dissolved oxygen were tested; each oxygen concentration-temperature combination was replicated ten times (Table V). The part of these experiments concerning the role of oxygen concentration on respiratory movements has a cross-like pattern, as this influence can be determined both by comparing the animals' behaviour at any one moment in bottles with different initial oxygen concentrations as well as by examining at regular time intervals the sets of bottles with the same initial oxygen concentration, since the oxygen content inside these bottles is gradually lowered by the animals themselves. The regression lines of respiratory

movements frequency in different oxygen concentrations and at 10.5°C, are showed in the Fig. 7. Each line is based on the results from ten larvae and the numbers of 1-min readings taken is given in Table V. As can be seen, the lower the oxygen concentration at the beginning of the experiment, the greater the frequency of respiratory movement. In all cases the frequency increased with prolongation of exposition time, e.g. with decrease of oxygen concentration in the bottles. The regression lines were more inclined in low initial oxygen concentrations. In the Fig. 8 the results for all three temperatures are presented in a condensed form.

Figure 8A shows the mean frequency respiratory movement (numbers per minute), together with their 95% confidence intervals, obtained from the ten animals observed at each temperature-oxygen combination. In general, the mean frequency is higher at higher temperatures but a reduction in the initial oxygen concentration raises the frequency of respiratory movements in all temperatures. The diagram of regression coefficients (a_1) — Fig. 8B, seems to confirm the above conclusion: the increment of respiratory movements with exposition time, expressed by regression coefficient (a_1) is more intense in low initial oxygen concentrations and in high temperatures. So one can take as proven that the worsening of respiratory conditions by heightened temperature or lowered oxygen concentration causes an increase in frequency of respiratory movements. The respiratory movements are then an adaptation of the animal enabling it to regulate its metabolism in poor respiratory conditions.

SUMMARY

The paper is a review of recent work on respiration executed by the staff of the Department of Experimental Hydrobiology, M. Nencki Institute of Experimental Biology, Warsaw, Poland.

The cumulative cost of maintenance of five species represents 36 to 79% of cumulated assimilated energy.

The errors involved in two methods of determining the oxygen consumption of animals are discussed. Flowing-water methods are recommended for aquatic animals.

The body weight–respiration relationship is presented for 8 species whose live weight ranged between 0.001–50.000 mg.

Two examples of allometric increase of oxygen consumption with growth and development of organisms are presented. During the development of *Rhizoglyphus echinopus* (Acarina) the resting stages alternate with active stages. The increment of the oxygen consumption in the resting stages is slowed down in comparison with the increment of the oxygen consumption of the active stages. The increase in oxygen consumption per weight increment was less in the nauplii of *Macrocyclops albidus* (Copepoda) than in the older stages of that species.

The influence of quantity of food on oxygen consumption of two carnivorous species: *Dileptus cygnus* (Protozoa) and *Macrocyclops albidus* (Copepoda) is discussed.

Three ways of calculating energy used are presented using actual experimental results. The variety of metabolized substances is taken into account in different degrees in each calculation.

The dependence of oxygen consumption of *Anax imperator* (Odonata) on the oxygen concentration is visible in all oxygen concentrations. Below 23% of air saturation the oxygen consumption rate decreases more markedly.

Worsening of respiratory conditions by heightened temperature or lowered oxygen concentration results in an increase in frequency of respiratory movements of *Perlodes intricata* (Plecoptera).

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