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SYMPOSIUM
BIOENERGETICS OF AQUATIC ANIMALS

Polskie Archiwum Hydrobiologii existing as such since 1953, is a continuation of *Archiwum Hydrobiologii i Rybactwa* founded in 1926 under the editorship of A. Lityński; during the period 1926 to 1939 and in 1947, thirteen volumes of *Archiwum Hydrobiologii i Rybactwa* have appeared, volume XII, 3, 4, published in September 1939, being almost entirely destroyed due to war action.

The journal publishes original works reporting experimental results, descriptive works and theoretical investigations in every sphere of hydrobiology. The article must contain original research not already published and which is not being considered for publication elsewhere. Papers will be published in the official Congress languages of Societas Internationalis Limnologiae (at present: English, French, Italian and German).

NOTICE TO AUTHORS

About manuscripts preparation principles will be printed in the last number of 1970, together with the yearly contents.

This issue contains papers presented at the symposium "Bioenergetics of Aquatic Animals" which was held on December, 10–14th, 1968 in Warsaw to celebrate the 50th Anniversary of the Nencki Institute

INTRODUCTION

The ceremonies concerning the 50th anniversary of the Nencki Institute of Experimental Biology took place between 9.XII.1968 and 12.XII.1968. Together with the Jubilee Session and the Plenar Scientific Meeting also the Symposia concerning the *Biological Membranes, Control Mechanisms of Behaviour, Physiology of Motor Response in Protozoa* and *Bioenergetics of Aquatic Animals* took place. More than 600 Polish and foreign scientists took part in the Jubilee Session as well as subsequently in the following individual Symposia.

The present part contains lectures and communications delivered at the Symposium *of Bioenergetics of Aquatic Animals* in the same form as they have been delivered at the Symposium. Moreover, an article of R. Z. KLEKOWSKI, Head of the Department of Experimental Hydrobiology is published showing the history and the present state of studies in the field of hydrobiology and bioenergetics, that have been conducted in the Nencki Institute of Experimental Biology during the last 50 years.

The organizers of the Symposium wish to express their gratitude to all of these who have celebrated the jubilee of the Nencki Institute and took an active part in the works of our Symposium. We also wish to express our thanks to those who helped to ensure the efficiency of the meetings and especially to chief organizer, Mr. JANUSZ WILTOWSKI.

SPEECH MADE BY DR. JULIAN RZÓSKA IN WARSAW
50th ANNIVERSARY OF THE NENCKI INSTITUTE
9 DECEMBER, 1968

Ladies and Gentlemen,

In the Polish preamble that I have just given I mentioned that the Organizers of this Anniversary Meeting invited me because they remembered that in pre-war years I worked in two of the stations that were part of the Nencki Institute. Though circumstances have separated me from the actual scene of Polish hydrobiology, which is part of the Nencki Institute's activities, our links have never been severed, and in an international sense they have now been intensified.

The hydrobiological part of the Nencki Institute is devoted to bioenergetics in the aquatic habitat. This is the field in which normal international scientific exchanges have been accentuated by the activities of the International Biological Programme.

The aims of the International Biological Programme deal with the "biological basis of productivity and human welfare". One could say that this is environmental biology concerned with Man and his surroundings. It is, I believe, for the first time in the history of scientific co-operation that biology has reasserted itself in a global programme against some of the geophysical and nuclear sciences.

In the development of hydrobiology, the production of organic matter and its passage through the successive steps of the food web of the ecosystem begin to emerge as a direct development of hydrobiology. The aims are perfectly clear and the principle of energy flow is simple as a concept, but the execution is extremely difficult.

A lake lying in the landscape is, as we know, a going biological concern; its water is a nutrient solution penetrated by sunlight which puts into motion plant and animal life. We know that a lake is a self-adjusting system and we know the principles upon which it works, but not the details. Yet we m u s t know, because Man's interference is increasingly creating biological spasms in nature, foremost by pollution. The enrichment in nutrients, not to speak of toxic substances, causes both decline and explosions of life in which some species that are more tolerant emerge, while the diversity of water life disappears. This is a highly undesirable effect.

On the other hand, the increase of production of certain species with the elimination of others is highly desirable and necessary in agriculture and fish culture. The two examples show clearly the necessity for steering human activities in a reasonable and selective way.

In order to use the natural environment so as to derive the necessary benefits without destruction, we must know the inner workings of the ecosystems — here in this context the workings of inland waters.

As the Scientific Co-ordinator of the Freshwater Productivity Section of the International Biological Programme, I work as the executive of a Section Convener and an International Sectional Committee. The present Convener,

Professor G. G. Winberg (Leningrad, U.S.S.R.) has contributed greatly to our understanding of production processes in inland waters. Previously, a Swede, an Italian and an American have presided over the PF Section in succession. The PF Section comprises about 360 projects undertaken by 38 nations and these are devoted to inland waters. These projects form a mosaic of different approaches according to the possibilities of the scientific manpower available and specific local problems. The level of investigation is very uneven in view of the state of hydrobiology in various parts of the world.

In order to raise the level of investigation, the IBP has elaborated manuals of methods. The PF Section has three in print; working meetings and symposia are arranged for the exchange of results and viewpoints. The next working meeting takes place in Leningrad (U.S.S.R.) and deals with the role of micro-bial activities in fresh waters. The services of consultants and exchange visits amongst workers in different fields are being arranged and training and cali-bration centres are planned.

The most difficult problem in production studies is, as already has been said, the links between the different trophic levels of primary, secondary and terminal phases, which make a lake a working unit. A partial elucidation of this complex problem has only been achieved in a few exceptional cases.

An attempt to unite the manifold investigations now in progress under the IBP, and to summarize the results in a preliminary way, will be made in the spring of 1970 here in Warsaw, with the help of the local Polish IBP/PF Committee. It is fitting that this most important working and results meeting should be held here in Warsaw where so much work on bioenergetics has been carried out, as the present Symposium devoted to the subject shows. It is also a tribute to the great tradition of Polish hydrobiology.

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A SPEECH DELIVERED BY DR. ROMUALD Z. KLEKOWSKI ON THE OPENING OF THE SYMPOSIUM ON BIOENERGETICS OF AQUATIC ANIMALS, THE 10th DECEMBER, 1968

Ladies and Gentlemen,

In the name of the collaborators of our Department of Experimental Hydrobiology and my own, I have the honour to welcome you on this Symposium. I welcome especially cordially our guests from other countries who had enough time to come to our jubilee.

Dr. DUNCAN from the Royal Holloway College, who has been so many times in our department, working with us and sharing our troubles and joys, is more one of the hosts here, than a guest. Dr. IVANOVA from Leningrad, who has also worked with us on the respirometer and microscope. Dr. PHILLIPSON from Oxford, whom the ecological bioenergetics owes so many valuable ideas, and whose part taken in the bioenergetic course IBP our department remembers with such gratitude as well as the calorimetric determinations that come from a microbomb devised by him. Dr. RZÓSKA — scientific co-ordinator of PF-IBP from London, has special reasons to feel at home at our jubilee, as he has been among those who in the Wigry Hydrobiological Station made the foundations of the Polish hydrobiology. Professor WINBERG from Leningrad honoured us with his presence, the works of whom — it is difficult to imagine contemporary bioenergetics of aquatic animals without them — shall be mentioned more than once at our Symposium. I welcome Professor ZEUTHEN from The Carlsberg Institute in Copenhagen; I have the pleasure to add my personal thanks for the hospitality I received in his laboratory and for teaching me beautiful respirometric methods which constitute now a port of our "arcenal".

I welcome hydrobiologists, ecologists and bioenergeticists from the whole country. It is a great honour for us that so many papers shall be presented here, and shall be included in a separated edition of the Polish Archives of Hydrobiology devoted to this Symposium. It should be stressed that although our Institute is celebrating its 50th birthday, our Department of Experimental Hydrobiology is still a "teenager". This does not mean, however, that we feel "illegal" at this symposium and this because of the fact that hydrobiology in the Nencki Institute, or more exactly — the hydrobiological Wigry Station is only two years younger than the Institute itself, which has also created the remaining hydrobiological stations, that were active between the two wars in Poland: the Sea Station and the Polesie Hydrobiological Station. So let this Symposium be in the honour of those who created these stations, unfortunately they are not longer among us.

I hope that our deliberations shall be fruitful and shall contribute to the further development of bioenergetical studies, which occupy such an important place in the programme of the International Biological Programme.

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SPEECH MADE BY DR. JULIAN RZÓSKA AT THE SYMPOSIUM OF BIOENERGETICS OF AQUATIC ANIMALS THE 12th DECEMBER, 1968

I came to the Anniversary Meeting and the Symposium as a co-ordinator of the Freshwater Productivity section of the International Biological Programme. The confrontation of an organizer with research workers and their work is necessary and beneficial.

Indeed, my ability to assimilate so many lectures and communications with intricate diagrams in a short time is rather limited, still a general impression remains and indicates how dynamic and rich in talents is the present day Polish hydrobiology.

Listening to this I formulated some notices and desiderata. First of all, I think about the necessity of uniting the mosaic of particular papers into more general compilations and recapitulations; further I think about the desired integration of bioenergetical investigations on particular organisms into the whole of productional studies. Then it would be indicated that the methods used here in bioenergetical investigations were rendered accessible to a larger circle of hydrcbiologists working within the IBP. It should be also proposed to accelerate the publication of communications delivered at this Symposium. Many of them are of importance towards the securing of aims of the Freshwater Productivity section of IBP and in view of a limited duration of our Programme one cannot wait for the normal, sluggish diffusion of printed papers. I am encouraging the organizers to collect and copy competent summaries, that is, containing the results and addresses of authors and spread them with the help of the PF section. This action would undoubtedly be valuable towards raising the level of work in many IBP centres, it would influence advantageously the international co-operation and would particularly help many investigators working away from larger scientific centres.

For all these reasons, and especially for the reason of the high level of the Symposium I consider my stay here very profitable.

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G. G. Winberg

ENERGY FLOW IN AQUATIC ECOLOGICAL SYSTEM

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ABSTRACT

The principles of working out a dynamic energetical budget of a total aquatic ecosystem are discussed basing upon the example of Lake Driviaty. The study comprised the biomass, production, destruction, consumption and assimilation of the main ecological groups classified according to the main trophic levels, over the vegetative period. The coefficients of production efficiency of these groups and trophic levels were also calculated as ratio of their production to biomass and assimilation. The relevance of coefficients of energy conversion for the evaluation of production efficiency of the ecosystems is discussed.

It might appear that the research of the International Biological Programme covers the whole ecosystem, thus also all phases of production process. This no doubt is true in theory; in practice, however, the organization of such a work meets considerable difficulties. The subdivision of all species into trophic levels is one of the main principles in the investigation of ecosystem productivity. This enables both "energy flow" and effectiveness of its use in various phases to be expressed quantitatively. This may be referred to both aquatic and terrestrial ecosystems, but in the present report only aquatic ecosystems are discussed, mainly with respect to their characteristic properties.

In practice, considerable difficulties arise due to a fact that the research of an ecosystem may be carried out only under the co-operation of various specialists in biology, i.e. zoologists, botanists and microbiologists, who follow various research traditions and apply various research methods. To use the results of numerous specialistic examinations in study on the "energy flow" in an ecosystem, the following simple principles should be taken into consideration.

1. The results of all botanical, zoological and microbiological experiments must be expressed in the same standard unit, or in units that might easily be converted into the standard one. Calory may be recommended as a general unit here. When other units are employed (dry weight, fresh weight, weight of organic matter, weight of organic carbon, and others), it is necessary to explain how to convert them into calories.

2. Methods and technique of sampling should assure proper presentation of total amounts and biomass of a given component in the whole ecosystem of

a water basin. However, the values presented in this way are uncomparable with the analogous data of the other water basins. Thus, they should be distributed according to the area of the basin and shown, for example, as kcal/m².

3. Where it is possible, the investigations should result not only in static values (number of individuals and biomass), but also in such physiological descriptions of organisms (objects) as rate of growth, intensity of metabolism, and others, which must be known to express trophic mutual relations of the ecosystem components, quantitatively.

As an example of applying such principles may serve here studies on the ecosystem of Lake Driviaty, Byelorussian area, carried out in summer 1964. The research was carried out by a team of hydrobiologists and ichthyologists under the leadership of the present author. The individual fragments of the research were conducted by the following students: R. Z. KOVALEVSKAYA (primary production of plankton), T. M. MIKHEEVAYA (phytoplankton), G. F. ZAKHARENKO (aquatic plants), J. S. BELYATSKAYA (bacterial plankton), G. A. PYETSHEN, W. A. KOSTIN, J. E. BREGMAN (zooplankton), S. I. GAVRILOV (zoobenthos), P. G. PETROVITSH, P. S. NEVYADOMSKAYA, A. L. SHTEINFELD, A. I. GOSHTSHEVSKI (ichthyology and fish feeding). A detailed presentation of the results of this research is now in print.

The eutrophic Lake Driviaty is 5.9 m in depth, its area being 3260 ha. The investigations were conducted throughout one summer period, from June to September 1964. Photosynthesis of plankton (primary production), rate of oxygen absorption in water, contents of chlorophyll, and distribution of solar radiation energy in water were studied in detail.

The amounts of bacteria in water and the rate of their reproduction were determined using a method of direct counting, broadly applied in the Soviet Union. This gave a possibility to calculate production of bacterial plankton. Species composition of zooplankton was determined, the quantity and biomass dynamics was estimated, as well as the production of the main species of crustaceans and rotifers. Similar data were obtained for benthos, as well. The results acquired during the ichthyological investigations, and those from the industrial statistics allowed both fishing and fish biomass to be estimated approximately.

All data necessary for a complete description of the ecosystem of the lake considered cannot be obtained during so a short period of investigation. Both rate of inflow of allochthonous organic matter and rate of outflow of this matter have so far not been determined. However, there is no basis to consider these the values from this lake highly important. Consequently, according to the data obtained, we can observe only the main features of the ecosystem. These results may barely demonstrate the method of investigation of the ecosystem and, on this basis, may help in selecting the unexplained problems to be solved in the future.

Table I and Fig. 1 gives the results of the investigations. During the calculation of the values presented in the table, some assumption and simplifications proved to be necessary. In consequence of this, the table illustrates only the approximate data determined with various degree of accuracy.

All the figures shown in the table are related to the summer period of the year, to a vegetative season, when the lake is ice-free. As a rule, this period lasts more than six months. However, due to the fact that, in spring and in autumn, water is characterized by low temperatures, we may assume

Table I. Biological balance of Lake Driviaty

	B	P	P/B	P/A	T	T/B	A	R
Primary production								
Phytoplankton	55	1200	22	—	300	5.5	1500	—
Macrophytes	80	100	1.25	—	20	0.25	120	—
Periphyton	?	120	?	—	30	?	150	—
Total	—	1420	—	—	350	—	1770	—
Bacterial plankton	7.2	442	61	0.5	442	61	884	884
Zooplankton								
Filter feeders	6.06	120	20	0.4	180	30	300	375
Predators	3.45	31	9	0.4	45.5	13.2	76.5	96
Benthos								
Non-predacious	2.11	6.5	3.07	0.3	15.1	7.2	21.6	27.0
Large molluscs	15	4.5	0.3	0.3	10.5	1.5	15	10
Predators	0.68	2.5	3.68	0.3	5.8	8.5	8.3	10.4
Microbenthos and bottom bacteria	?	?	?	?	?	?	?	?
Fish								
Non-predacious	19	7.5	0.40	0.2	30	1.6	37.5	47
Predacious	5	1.5	0.30	0.3	3.5	0.7	5	6

Explanations: B — biomass, kcal/m², mean value for vegetative period; P — production during vegetative period, kcal/m²; T — destruction, kcal/m².; A — assimilation (assimilated food), $A = P+T$; R — ration, $R = A\frac{1}{U}$, where $\frac{1}{U}$ — assimilability of food, $1/U = A/R$.

the vegetation period to last about 150 days, its temperature being about 20°C. Such an assumption simplifies certain useful approximate calculations. For each component of the ecosystem, the Table gives: mean biomass (B) expressed in kcal/m², production (P), destruction (T), i.e. energy losses for energy exchange, assimilation of food ($A = T+P$), and ration (R), expressed in kcal/m² for a summer period.

The production is understood here as net production, i.e. as a sum of increases in the individuals of all species, comprised in a given trophic level, including also these individuals, which did not survive the whole summer period in study. It may be thought that this is a generally accepted definition of production here.

Destruction, in this case, does mean the total loss (dispersion) in energy by the organisms in a given trophic level. The destruction represents the total effect of energy losses for metabolic processes of the representatives of all species that belong to the given trophic level.

Assimilation, also called gross production, is the sum of production and destruction, or means the total amounts of the food assimilated ($A = P+T$).

The total amounts of necessary food, or ration (R), may be calculated when both assimilation (A) and assimilability of food $\left(\frac{1}{U} = \frac{A}{R}\right)$ are known, since $R = UA$ ration is equal to the assimilation divided by food assimilability. The food assimilability represents fraction that illustrates how much of the food eaten is assimilated. During the experimental research of feeding among
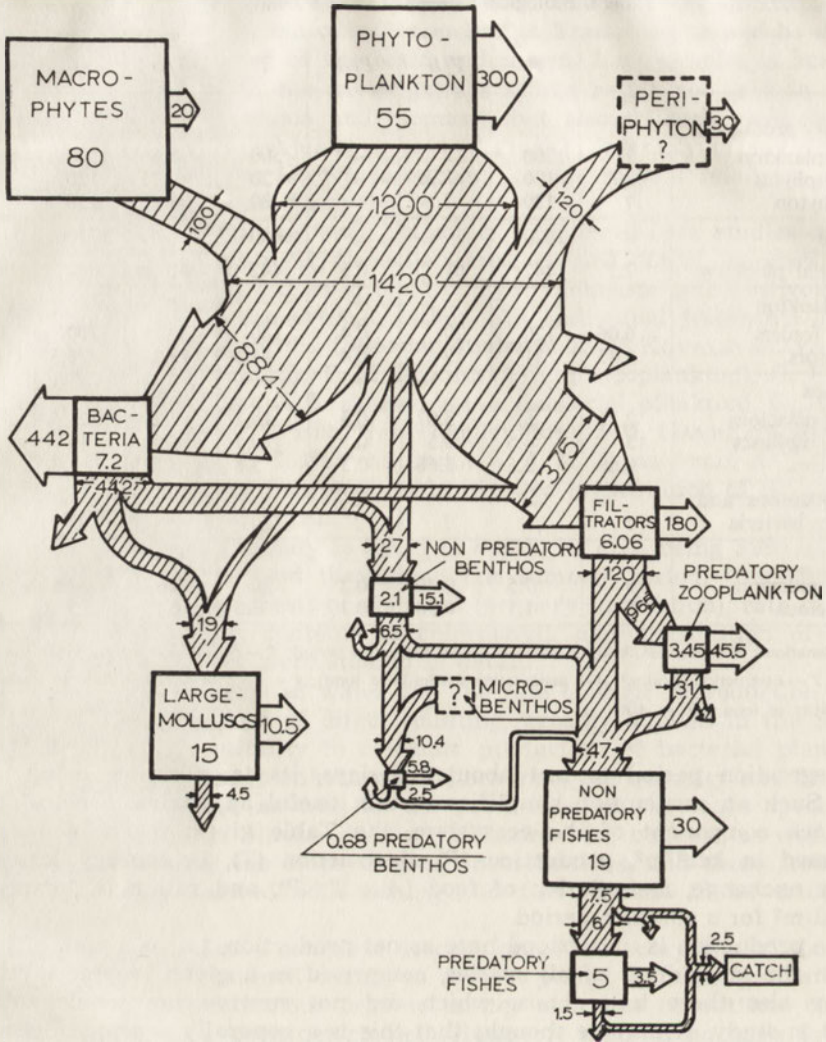
Fig. 1. Energy flow diagram for Driviaty Lake. Figures in kcal/m²·veget. season, numbers inside boxes indicate biomass; number inside arrows = destruction i.e. cost of maintenance; numbers indicate the width of the shafts = production or consumption (food intake)

aquatic animals, e.g. planktonic crustaceans, low values of assimilability were observed by various research workers. However, during the highly precise examinations, when the kind of food corresponded to the requirements of the species investigated, high assimilability was noted. Most probably, under natural conditions, a high food assimilability is a general rule among the freshwater animals. Thus, this property among planktonic and benthonic animals and among fish individuals is equal to 0.8 (that for pre-

dacious fish amounting to 0.9). If $\dfrac{1}{U} = 0.8$ then $R = 1.25\ A$. As it may be seen later, the results obtained satisfactorily correspond to this assumption.

P, A and R values are expressed in kcal/m² for the whole summer period. As it was previously mentioned, we may suppose that it lasted approximately 150 days, the temperature being about 20°C. The Table also gives ratios or coefficients where $K_2 = P/A$, P/B, T/B. There are ample evidences to ascertain that in such natural populations as, for example, freshwater zooplankton, which consists mainly of growing individuals (eggs included), the mean value of K_2 is, for this population, fairly high. In the case of zooplankton we have accepted that $K_2 = 0.4$, and $T = 1.50\ P$. For benthos, this value was $K_2 = 0.3$, on the average.

P/B represents here the mean rate of growth. For a population with the constant biomass P/B means "turnover rate" and B/P — "turnover time". When P and B are known, their ratio P/B can easily be found. Frequently, however, the coefficient P/B is thought to be known, and then it may be used in determination of production (P), according to the known value of biomass. This, in the case here considered, was used during the calculations of production of certain groups of benthonic animals.

Such a way of calculation gives satisfactory results, mainly due to the fact that the coefficient P/B is, for each given species and for given conditions, practically constant, or it changes insignificantly, whereas both biomass and production may differ considerably. In our case the production of certain groups of benthonic animals has been calculated according to the values of P/B coefficients taken from the experiments and from the literature.

T/B coefficient is proportional to the mean rate of metabolism (intensity of metabolism) of the individuals of all the species in the given trophic level.

The value T may be obtained in two different ways: 1) according to the known rate of oxygen consumption, and 2) according to the known ratio $P/T = K_2/(1-K_2)$ and P. Application of both calculation methods gives a highly valuable possibility to check the reliability of the results obtained.

At present, there are numerous data on the rate of oxygen consumption by aquatic animals. Particularly important are relations between the individual weight and intensity of metabolism ascertained by numerous scientists. For example, in studying crustaceans we used an equation as follows:

$$\frac{Q}{W}\ (\mathrm{mlO_2/g\cdot hr}) = 0.236\,W^{-0.19}(20°C),$$

where W is expressed in g of fresh weight. To express the intensity of exchange in calories it is sufficiently to know that oxycalorific coefficient is equal to 4.86 cal/ml O_2.

The second method is based on a fact that the rate of growth and that of metabolism are strongly linked up by a variously named coefficient that reflects the relation between the increase and assimilation of food:

$$K_2 = \frac{P}{P+T} = \frac{P}{A}.$$

It is evident that $T = \dfrac{1-K_2}{K_2}\,P$. In consequence of this, and when K_2 and

P are known, T may easily be calculated. There are already numerous experimental data at present that in many cases allow K_2 to be considered well-known. At our laboratory a series of experimental examinations in this domain have been made, too. The results of these examinations will as soon as possible be published. During the comparison of both methods of calculation, made for phytoplankton, bacteria and zooplankton, well comparable results were obtained. Now we shall discuss conclusions that may be drawn according to the data available.

Apart from the fact that all the data shown in the Table were obtained by various authors separately, and that numerous inaccuracies among them may appear, the table does not show any absurd relations, when comparing the values of various trophic levels, or when comparing the results from the Table which are obtained independently. This interesting and even unexpected result allows us to assume that the data presented in the Table have actual importance.

Unfortunately, the contents of the Table cannot in this paper be broadly discussed, and therefore only some remarks will be presented.

The value of the primary production corresponds to that of the medium-eutrophic lakes, to which also Lake Driviaty may be related, also due to all its another features. P/B ratio for phytoplankton is of interesting value here. The biomass of phytoplankton has been determined in two ways (according to the volume of cells, and according to the contents of chlorophyll, which amounted to 1.6 per cent of dry weight, on the average). Thus, an unexpectedly low P/B ratio of phytoplankton cannot be explained by a too high biomass value of phytoplankton, which may have been taken erroneously.

As far as bacterial plankton is concerned, two moments should be taken into consideration. First, it is worthy of being emphasized that the P/B coefficient, characteristic of the summer period, practically also of the whole year, reveals not too great values, equal to 61. This proves wrong estimations presented by certain authors, who have supposed that the P/B coefficient of bacterial plankton per year may be equal to such high values as 1000. This however, well corresponds to the results of the investigations made by the Soviet microbiologists with respect to the other lakes. J. S. Potayenko (1958) has ascertained that, for the mesotrophic Lake Naroch, this coefficient is equal to 49.4, and for the highly eutrophic Lake Batorin it amounts to 98.5. For the oligotrophic mountain Lake Sevan, M. E. Gambaryan has obtained a value that amounts to 18.3. Secondly, we see that the assimilation of bacterial plankton corresponds to a considerably high value equal to 884 kcal/m²; this corresponds to 62 per cent of the primary production of phytoplankton. In fact, at such a production this value must always be higher, mainly due to the minimum possible value of bacterial metabolism taken into account, because it has been accepted that for the bacterial plankton T is equal to P, i.e. the growth of bacteria proceeds with the considerably high effectiveness of use of food energy ($K_2 = 0.5$).

Such a considerable participation in the energy flow within an ecosystem cannot be thought to be unexpected. Analogous conclusions may be drawn on the basis of the other examinations made by the Soviet scientists with respect to another lakes and water basins.

The value of zooplankton biomass was obtained by means of common hy-

drobiological methods, and that of zooplankton production — with the aid of the calculation methods recently worked out in the Soviet Union (Methods, 1968). To know the production of a population of a given species, one has to determine the individual weight characteristic of various development stages, the length of a stage under given conditions, and the number of individuals in the given stages of development.

A high P/B coefficient of zooplankton, which corresponds to the mean value of P/B coefficients calculated from the individual species, may be perceived, similarly as a considerable production, significantly higher than that of benthos. High is also the ration (food consumption) of zooplankton, apart from the fact that for its determination a high assimilability, equal to 80%, has been taken into account. Of considerable significance is here a fact that the ration of zooplankton proved to be lower than the production of bacterio-plankton. This is an evidence of the fact that bacteria play an important role in the feeding process of zooplankton. Interesting is also that the ration of zooplankton predators is only slightly lower than the production of the non-predacious species. In consequence of this, a great deal of production of zooplankton filter feeders is consumed by predacious species. This is a very important fact illustrating highly strained feeding relations in the zooplankton association.

Hence, a question arises, how to determine the production of the whole zooplankton association that consists of two trophic levels at least. Theoretically, this production should be equal to that of filter feeders, minus the ration of predators, plus their production. In our case it was equal to 56 kcal/m², i.e. 46.5 per cent of the production of filter feeders. Unfortunately, the exactness of this value is low, since it represents only the algebraic sum of three magnitudes charged with their own errors. However, it is worthy of being emphasized here that the calculated value of the whole zooplankton production proved to be greater than the ration of fish, i.e. it was sufficient to meet their food requirements.

As far as benthos is concerned, we may say that its biomass is two times higher than that of zooplankton, whereas the production is many times lower. Particularly high is the value of biomass of large bivalve molluscs, but due to a low rate of their growth the production is insignificant.

The total ration of all non-predacious benthonic animals is small, many times lower than the primary production, and the production of bacterial plankton. The total production of the non-predacious benthonic species (without large molluscs) is lower than the ration of the predacious ones. This is an evidence that microbenthos, the production of which has not been investigated, is of considerable importance in the feeding processes of predacious benthos.

Figures that concern biomass and production of fish are not precise, since only standing crop of fish, equal to 2.5 kcal/m², was examined more in detail, fish biomass being determined rather on a small scale. Apart from their inaccuracy, these figures allow us to draw important conclusions. In terms of energy, the total standing crop of fish is only 0.14 per cent of the gross primary production. The total non-predacious fish production amounts to 0.4 per cent of the primary production, and the fish ration, i.e. the whole consumption energy of food for a summer period amounts to 2.65 per cent only. These figures, corresponding to the previously known relations, demonstrate once

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again that fish assemblage only slightly participates in the energy flow of the
lake ecosystem.

There is nothing new in this opinion. Such a conclusion may have been
drawn already according to the data presented by other authors, too. Thus so
much the more considerable significance may be attached to the conclusions,
which may be drawn from this unquestionable fact. It distinctly points to the
insufficiently presented evidences on the energy flow, mainly as concerns the
final links of food chain, which, from the practical point of view, are more
interesting for man. This means that a description of energy flow cannot be
the only or the main task in studying the productivity of the ecological sys-
tems.

The study of the ecological systems, conducted from the energy point of
view, is of fundamental importance when determining the characteristic featu-
res of biotic balance in the ecosystem of a given type. This is an important
and indispensable task of limnological studies, since only in this way a range
may be elucidated of various biological phenomena that determine the total
biological productivity of a water ecosystem. In relation to the final products
useful for man, a description of energy flow in ecosystems seems not to be the
final purpose of the investigations. These are only a basis for detailed biolo-
gical analysis, which requires the application of other biological methods, first
of all, the knowledge of quantitative ecology of the most widespread species
of water organisms. When studying the quantity, biomass, and production of
various species populations, we have to use population ecology methods, in-
sufficiently introduced into the hydrobiological studies, however.

The practice of fish industry has demonstrated that by means of various
fishing industry methods affecting the final trophic level (fish) we may incre-
ase fish productivity of a lake. Thus, the difficult and little known problem of
influence of the higher trophic levels upon the lower ones seems to be of espe-
cial importance; particularly the system of fish exploitation in a lake, affecting
its animal and plant populations, its productivity, and biotic balance of both
matter and energy.

All these complex problems are not dealt with in this report, however. The
report aims only to demonstrate the general scheme or methods of quantita-
tive analysis of the energy balance in the ecosystems of eutrophic lakes, and
to present a rough scheme based on not too accurate data. Nevertheless, some
general conclusions may be drawn. The method under consideration can also
be applied when more complete and precise data are available; in consequence
of this also better results may be obtained. The main principles of this me-
thod, i.e. the physiological and ecological notions, which are used for determi-
ning the budget of energy in an ecosystem, require more precise definition,
however.

First of all, thorough experimental studies should be developed to explain:
a) the quantitative relations between the rate of growth, intensity of exchange,
and food requirements (rate of feeding), and b) the dependence of intensity
in metabolism upon the weight of body and upon the main conditions of the
environment.

As far as the most widespread species of water organisms are concerned,
systematic, thorough research should also be developed on a large scale to
explain some features, characteristic of a given species, such as values of dry
and fresh weight, calorific value in various stages, rate of growth, intensity

of metabolism, fertility, dependence of feeding rate upon food concentration, assimilability of food according to the main conditions of the external environment, and others.

The knowledge of these properties allows us to describe quantitatively the energy flow in ecosystems more in detail. Although this cannot be the final aim of the research on biological productivity, it may serve as an indispensable general basis to explain the problem here considered.

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E. Zeuthen

RATE OF LIVING AS RELATED TO BODY SIZE IN ORGANISMS

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ABSTRACT

The author, basing mainly upon his own investigations of metabolism intensity (respiration) chiefly of planktonic animals and their larvae, defines the fundamental types of relations between the respiration intensity and body size of organisms ranging from bacteria to large poikilothermic and homeothermic animals. The slope of the regression of metabolism on body size was particularly discussed as well as the resulting conclusions about onto- and phylogenetical mechanisms of conditioning the animal size.

> *"and thus do we of Wisdom and of reach with wind lasses and with assays of bias by indirections find directions out".*
>
> William Shakespeare, "Hamlet", act 2, scene 1, verse 64

Though I am not a hydrobiologist in the strict sense of the word, Dr. R. Klekowski has invited me to speak in this symposium on hydrobiology in celebration of the 50th anniversary of the Nencki Institute. I have to dig far back in my past to justify my being here, and I shall discuss some work I did during the second world war when confined to the Island of Zealand in Denmark. I then did hydrobiology, working under the bastions of Kronborg Castle in the town of Helsingør, the Elsinore of Shakespeare's Hamlet.

The story I am going to tell you begins with measurements of oxygen uptake in the range of quite small animals, only a few tenths of a millimeter long. The results obtained differ significantly from what would have been expected from extrapolations into this range of organisms from previous observations made for larger animals for which approximation towards surface-consumption relations are the stated rule. This report begins with measurements of oxygen uptake in single marine veliger larvae, but the studies will expand, and I intend to discuss general relations between the size of organisms and their total oxygen consumption per unit time, or their rate of oxygen consumption per unit time and per unit body-nitrogen. I will do this from the point of view of a general physiologist and an amateur evolutionist. Let it be said at the beginning, that I have seen few differences in

relations between oxygen consumptions and sizes of organisms, regardless of whether size variation results from ontogenetic or phylogenetic increase in body size. This makes me use the two latter words rather freely, if not too freely.

What induced me to spend three summers in Dr. GUNNAR THORSON's small field laboratory in Helsingør — the nucleus for the bigger laboratory now existing — was current ideas that the veliger larvae of marine snails and bivalves had to spend immense energy in keeping themselves suspended in the free waters by active swimming. The telling was that the amount of oxygen consumed per unit weight by the swimming veligers would be somewhere between 10 and 100 times what would be spent after the larvae had settled on the sea bottom. Practically no measurements were available to support these views, which indeed were mostly based on the consideration that the pelagic larvae possess a larval swimming organ, the ciliated velum, and that they are burdened with the fairly heavy larval shell.

In 1939 I got my degree as a Magister in comparative physiology from AUGUST KROGH's laboratory and went to work with KAI LINDERSTRØM-LLANG and HEINZ HOLTER in the Carlsberg Laboratory, both then engaged in developing the Cartesian Diver Respirometer. In Helsingør Dr. GUNNAR THORSON sat with his nagging doubts about how to divide the total energy consumption of the small marine animal life on pelagic and bottom life. I seemed fit to supply the answer and was invited to Helsingør to do the job. So I set up in THORSON's laboratory, in reality a candy shop in the basement of one of the pretty old houses in the harbour of Helsingør, available in war time for lack of candy.

The Cartesian standard diver, in LIINDERSTRØM-LANG's and HOLTER's classical edition (HOLTER 1943, LINDERSTRØM-LANG, 1943) appeared excellently suited to studies of marine organisms in the size range of veliger larvae. In most cases one or only a few organisms were enough to produce suitable pressure changes with handy 10 μl divers. Whenever possible (for me) the species of the larvae were identified from THORSON's then new treatise on the subject (THORSON 1946), and after the experiment the larvae were sealed up with H_2SO_4 in a piece of glass capillary for later measurements of body-N, with a micro Kjeldahl method (BRÜEL et al. 1946). The first summer I harvested data for oxygen uptake per specified organism at 20°C, but only in the winter did I obtain the corresponding ratios $O_2/N \cdot hr$, which would permit comparison of oxygen uptake between plankton and bottom forms of equal and different body size. Waiting for these data I stuck other experiments in, using the 20 times more sensitive capillary diver, a modification of the standard diver (ZEUTHEN 1943).

These other experiments in effect supplied the information asked for. In Figure 1 you see results of three runs with single veligers of Mytilus, Zirphaea and Mya. The two latter were continuously resting in the diver, but the Mytilus larva occasionally swam about for periods long enough to supply measurements of the metabolism of a swimming larva. The rate of oxygen uptake increases by less than a factor 2 when the resting larva gets swimming. This experiment is repeated in the upper curve of Figure 2. The larva was then removed from the diver and the velum chopped off using the valves as scissors. Contrary to what happens in the intact larva, the isolated velum swims about continuously, and the rate of metabolism is just the dif-
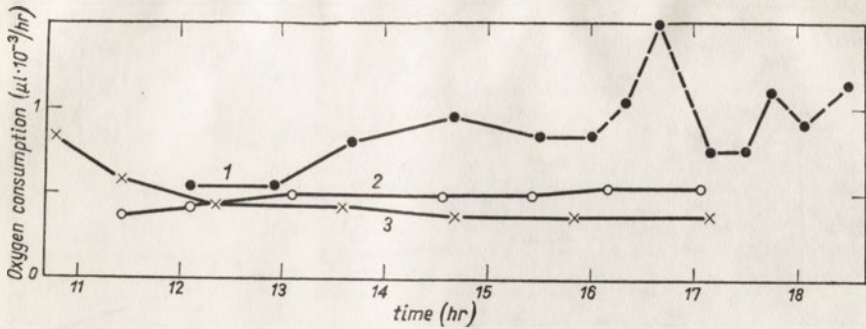
Fig. 1. Lamellibranch veliger larvae from the marine plankton. Variations in respiratory rate (ordinate) during sustained experiments. 1 — *Mytilus edulis* (length 0.235 mm), 2 — *Zirphaea crispata* (0.214 mm). 3 — *Mya arenaria* (0.170 mm). From ZEUTHEN 1947
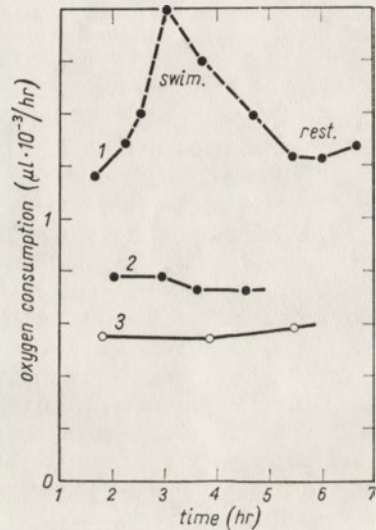

Fig. 2. Veliger of *Mytilus edulis* (length 0.25 mm). 1 — rate of respiration changes with transition from rest to swimming, 2 — rate of respiration of isolated velum from larva studied intact above, or 3 — from another Mytilus larva. From ZEUTHEN 1947

ference between the rate of the swimming and the resting larva (curve in the middle). Finally, other experiments showed that transition from rest to sliding movement on the substrate stimulates larval metabolism as much as does swimming. From these results can be strongly suggested that swimming taxes energy metabolism just slightly, and it can be suspected that the rate of metabolism of comparable planktonic and bottom forms is about the same in the sea.

By winter the ratios O_2/body-N could be established. The results for *Mytilus edulis* are shown in Figure 3. The most left, and highest, values are for 24-hours trochophorae, then follow results with veliger larvae, and to the right of the first dashed line experiments with newly settled larvae of different sizes. To the right of the second dashed line results are shown which
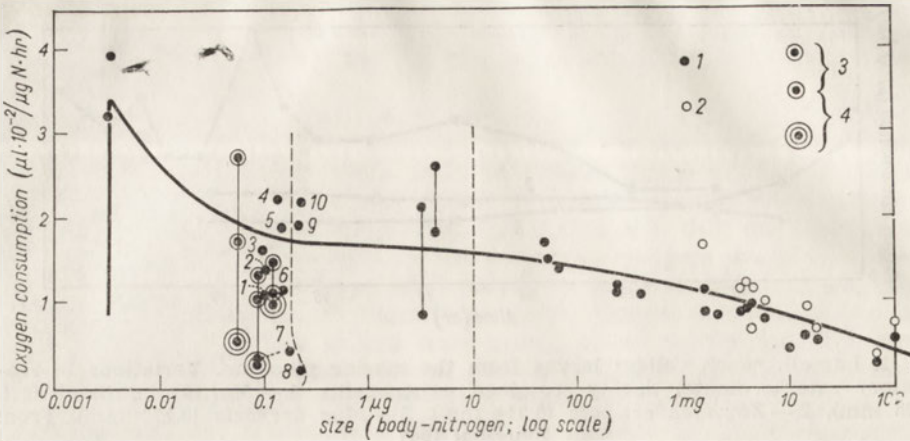
Fig. 3. Respiratory intensity (ordinate) of *Mytilus edulis*. To the left of first dashed line: Trochophorae and veligers. Between dashed lines: newly precipated larvae. To the right of second dashed line: young or older mussels. 1 — body-N in whole animals, 2 — body-N in tissues, 3 — range of rates when swimming, 4 — range of rates when veligers are not swimming

have been obtained with Winkler-experiments (oxygen titrations) in older and larger specimens (length $<$ 5 cm). The legend of the figure accounts for states of activities during the respiration measurements, and the conclusion is that the rate of respiration (O_2/N·time) decreases some, but surprisingly little, with increase in body size during development, and with age in this organism. Transition from planktonic to sessile life on the sea botom is not marked in the least. Apparently, the cost of ciliary activity of the velum in the swimming larvae is only replaced by the cost of ciliary activity of the gills of the filtering bottom animals. So, this was the answer to THORSON. These results have been of some value for the hydrobiologist qualitatively, but not of much value quantitatively. This comes from the sad fact that physiologists measure single organisms by size and ecologists measure populations by numbers, essentially disregarding individual size. Here is a gap for someone to fill in.

Only small decrease in rate of metabolism with increase in size was found also with other small marine animals and taxonomic groups, regardless of biotope and taxa. An example dealing with the vermes is in Figure 4, and a summary is shown in Fig. 5. The latter figure includes curves from the literature and essentially covers the Animal Kingdom, from the size of the smallest marine larvae to the size of an elephant (estimated at 100 kg N). Measurements based on live weight have been included in this diagram assuming that animals contain 1% body-nitrogen. Limiting ourselves to consideration of poikilothermic invertebrates and vertebrates studied at temperatures around 20°C (curves I–XI) we can trace some taxonomic differences and perhaps make some correlations with biotope, but the main variable is body size of the organism considered. This variation is tremendous, 11–12 decades. Indeed, the oxygen uptake per unit amount of tissue per hour does decrease much and rather smoothly troughout this range, how much and how smoothly shall be discussed. This graph also contains curve XIV, Benedict's famous
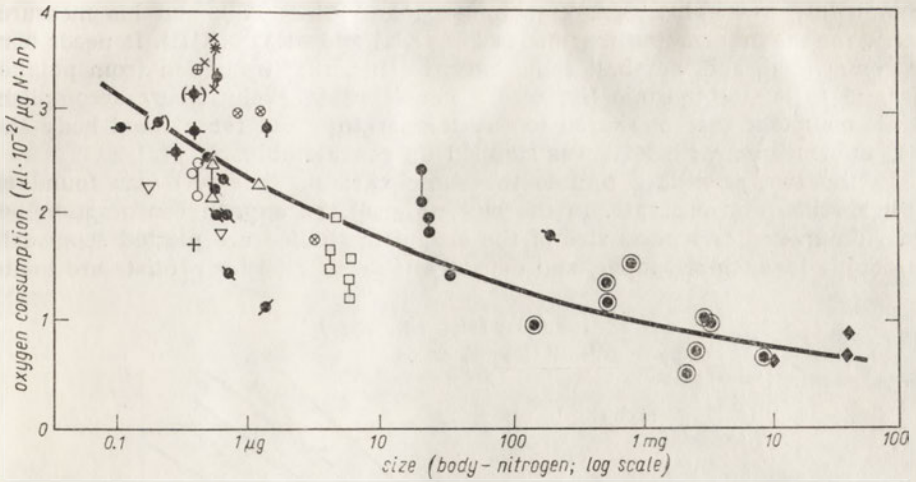
Fig. 4. Respiratory intensity (ordinate) in Vermes (18 species) from plankton and bottom of Øresund. Abscissa gives body-N. From ZEUTHEN 1947
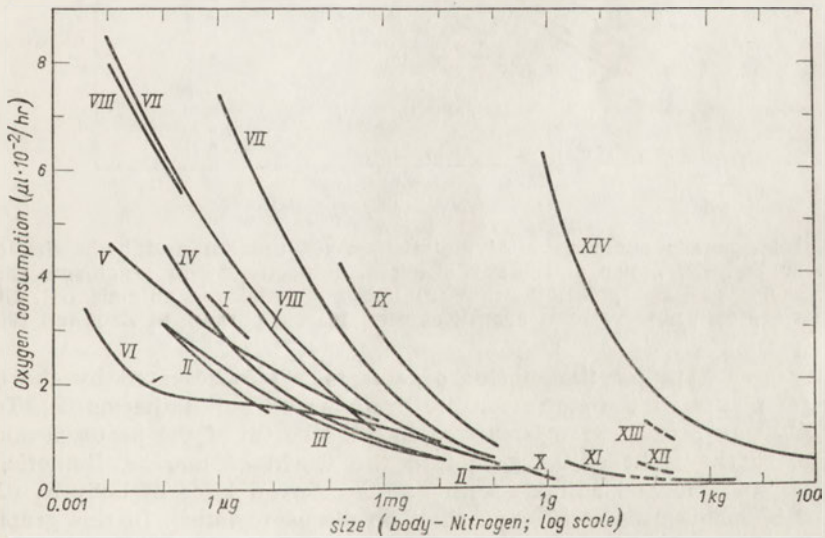
Fig. 5. Comparison of the metabolic rates of animals on the basis of body-N. Own data, and data collected from literature. From ZEUTHEN 1947. I — Coelenterata 16°, II — Asterias 16°, III — Vermes 16°, IV — Nassa 16°, V — Littorina 16°, VI — Mytilus 16°, VII — Crustacea 16°, VIII — Balanus 16°, IX — Pisces 16°, X — Frogs 20°, XI — Reptilia 20-25°, XII — Marmot 20°, XIII — Marmot 37°, XIV — Birds and mammals 37–40°

from mouse to elephant curve (mammals, and birds 37°), and his measurements for the hibernating marmot at 20° (XII) and at 37° (XIII). It needs here be commented, and we shall come back to this, that transition from poikilothermic to homoeothermic life was a considerable evolutionary accomplishment: metabolic rate measured at one temperature and for a fixed body size (XI, as compared with XII) was stepped up considerably.

In the two preceding figures the same variable (body-N) was found on both abscissa and ordinate. In the next (Fig. 6) the oxygen consumption per individuum and hour, and size of the organism studied are plotted separately on double logarithmic paper, and data available in 1952 for protists are inclu-
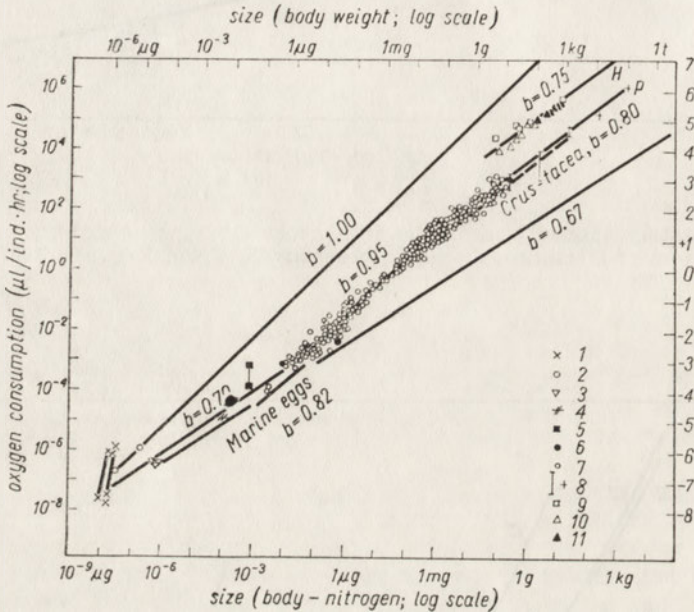

Fig. 6. Interspecific comparison of metabolism (O₂-uptake) and body size (fresh weight or body-N, upper and lower abscissa, respectively) in organisms ranging from bacteria to large poikilothermic (P) and homeothermic animals (H). Hollow points are own observations. From ZEUTHEN 1953. (Redrawn in ZEUTHEN 1967)

ded. My own data for the marine organisms are represented by the dense swarm of points on the curve for the protists and poikilotherms (P). To the left of 10^{-2} µg N this curve is carried into the realm of the protozoa and the bacteria, to the right of 0.1 g N into the world of marine, limnetic, and terrestrial cold blooded animals with grams or even kilos of body-N. (Curve H is for homoioterms at 37° and shall be discussed later). In this graph organisms with same (bacterial) rate of metabolism would fall on the straight line marked $b = 1.00$. Not surprisingly, all other points fall below this line. The protists and poikilotherms supply data which cover 17 decades on the abscissa, but only 13–14 decades on the ordinate. In brief, the metabolic rate of large cold blooded animals is in the order of 1000–10,000 times lower than the rate in bacteria. Nonetheless, the two rates are not fully independent. To see this, one needs look at the living world of protists and cold-blooded animals

as a whole. The size extremes are connected by a narrow band visible in this graph as a curve (P) which represents randomly collected samples from all living animal organisms, exclusive of the homoiotherms. Thus, body size and body oxygen consumption are correlated throughout the living world, but correlations are not simple. This shall now be discussed.

As you will notice, the band P in Figure 6 can not be described by a single straight line, but with approximation by three. The homoiotherm curve is represented by one line with roughly the same slope at the first and last piece of curve P. The slope (b) of these lines is 0.70–0.75. It represents the relation between the logarithms of the body size (abscissa, x) to those of the oxygen uptake per unit time of organisms as a whole (ordinate, y).

$$\log y = 0.75 \cdot \log x + \log a$$

$$y = a \cdot x^b, \text{ or}$$

$$O_2 \text{ consumption} = a \cdot (\text{body size})^b.$$

Constancy of b indicates that in mammals and birds the logarithmic or percentage change in y (metabolism) varies directly with the logarithmic, or percentage, change in x (body-N). The exponent (b) is the ratio of the percentage change in x, to the percentage change in y. In other words, in mammals 100% increase in body size gives 70–75% increase in total oxygen uptake. In a broad way, this same relationship holds true also for the poikilotherms (P), but only for bodies containing N above 1 mg or so, as roughly estimated from Fig. 6. It is true also for the protists ($N < 10^{-2}$ μg N) but it is not true for small metazoa (1 mg $> N > 10^{-2}$ μg). In these organisms 100% increase in body size gives 95% increase in metabolic rate ($b = 0.95$). These figures become more dramatic if one follows decrease in metabolic rate over large ranges of variation in body size. If we consider increase in size by a factor 10^5 in mammals and birds (10 g to 1000 kg wet weight) in poikilotherms (0.1 g to 10–100 kg wet weight) and in protists (10^{-6} μg to 0.1 mg wet weight) the decrease in rate is to 1/10 or 1/20. If, on the other hand we consider the range in which there is 10^5 times increase in size of the small metazoa (1 μg to 0.1 g wet weight) the decrease in rate is only to 1/2 or 2/3. This, I think, is an important generalization which has escaped most writers of text books in physiology. It follows from what has been said that increase in body size meets internal resistance in the sense that size increase is paid for by loss of rate in energy metabolism of each unit amount of tissue, but this resistance is much lower in the smallest and in small metazoa than in both protists and in larger metazoan organisms, poikilothermic or homoiothermic, and the size of bodies with net weight around 0.1 g and containing about 1 mg N separate between small and larger metazoa. I believe that these relations can have been of highest evolutionary significance, and to illustrate this we shall consider first curve P, then curve H in Figure 6, always going from small in the direction of larger body sizes. Thus, starting from the extreme left in the figure we observe that increase in size and in respiration in free cells obeys some sort of a Rubner surface-law. In these days this seems easier to understand than in the days before the electron microscope. Cells have lots of outer and inner membranes. I shall not discuss this further, only suggest that ontogenetic and phylogenetic size increase in the unicellular organisms met internal resistance (defined above) and that the evolutio-

nary response was the multicellular organisms. To make this a bit clearer, I will say that as cells got larger they tended to loose intensity for supplying and using energy, and at some point in the evolution of larger and larger cells, the solution was found to the problem how to make still larger organisms with reasonable rates of energy consumption: the solution was multicellularity. Once evolution had arranged this, further size increase could take place against little internal resistance, and over a broad range, in fact to the size of animals containing about 1 mg N. Why the approximate surface to oxygen-consumption relations as in the protists should reappear in animals growing above this critical size. I have no idea, and really, nobody seems to have. Speculations are plenty, and need not to be repeated here.
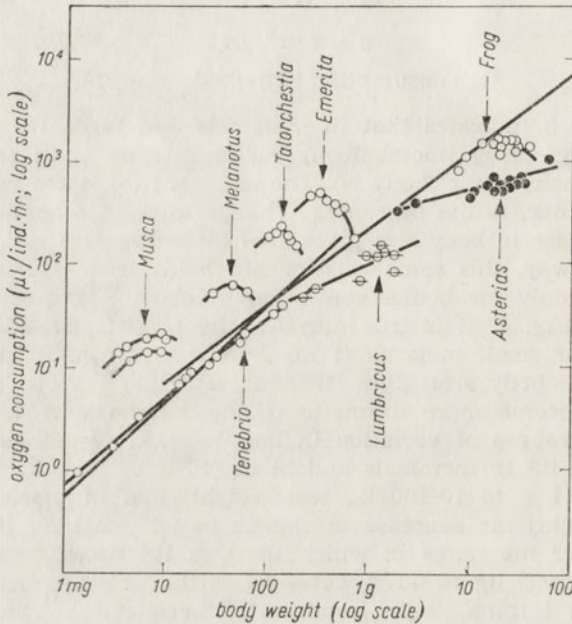
Fig. 7. Intraspecific comparisons of different animal species studied over size ranges near the final size of each species. Data from literature. From ZEUTHEN 1953. (Redrawn in ZEUTHEN 1967)

Can organisms outgrow their capacity for supplying the machinery which produces the metabolic energy? If so, would this in the end set a stop for further size increase in increasingly sluggish animals? Well, the question is not to be answered, but to press the issue I want to present a provocative plot of data fetched from the literature (Fig. 7). This figure shows interesting additions to the general rules, which I proposed in the discussion of Figure 6. This is possible, because the analyses shown in Figure 7 are more refined.

If we dare consider the band of observations represented by curve P in Figure 6 a picture of the evolution of body size and respiration in organisms, then Figure 7 indicates that the metazoan species hang as ripe fruits on the tree of evolution. The stem of the tree is a piece of band P from Figure 6. As seen, for each species there is the tendency that the metabolic rate drops

off as the species approaches its final, genetically fixed size limit. We shall not conclude that growth of a species is ultimately limited by energy, only that size limitation is reflected at the level of energy metabolism.

Now I want to return to Figure 6. I am fascinated, not only by the continuity of the observations in band P, but also by the jump on the ordinate from band P to band H, from the curve for large poikilotherms (measurements at around 20°C) to the curve for the homoiotherms (measurements at body temperature). As previously stated, this jump can not just be explained away as resulting from differences in temperatures at which measurements were made. It would be there anyway (cf. Fig. 5, XII–XIII), and it indicates an immensely important step-up of metabolic rates which may have conditioned the evolution of homoiotherm life. To understand how the jump could have come about, we need inspect Fig. 6 more closely. In this figure the continuous line to the right of 100 mg (abscissa) has a value of b close to 0.75. Ontogenetic size increase in the frog (Fig. 7) appears to obey a value of b near this up to a larger size than in any of the other species shown in this figure. This can be considered a success on the part of the frog, because any lower value of b would have given the frog a lower rate of metabolism than a frog actually has, or frogs the size of frogs might not have existed. In the same sense, the crab Emerita was smarter than the amphipod Talorchestia, and this species better than the insect larva Melanotus. Before we continue, please remember that ontogenetic and phylogenetic size increase can take place at a minimal cost paid in decreased rate of metabolism only when b is near unity. We are discussing the transition from poikilothermic to homoiothermic life, and what I am now proposing is that genetic change in the earliest birds and mammals let these forms acquire capacity to maintain high values of b over a broader ontogenetic range of size increase than possessed by their ancestors, and that this gave the early birds and mammals a high rate of metabolism compared to that of other equally sized animals, and enough heat production per unit of surface to permit development of elevated body temperature and of thermoregulation, further steps in the direction of increasing the energy output per gram of body weight. From this platform homoiothermic life may have developed, taking advantage of the fact that basic laws existing before the homoiotherms appeared cn the scene dictated that energy production must increase less than body weight, but more than body surface $(1 > b > 2/3)$.

In other words, once homoiothermy was there, development was from forms which just managed to keep warm to large forms which rather faced problems of how to get rid of their metabolic heat. To me this is the situation as it exists to-day. Really, to see these points illustrated one needs only extrapolate the line P with slope 0.95 in Fig. 6 to intersection with line H, which slopes 0.75, and in addition make reasonable correction for differences in temperature of bodies studied. Which animals are on this extrapolation? The answer is simple: the embryos of all mammals (Brody 1945) and birds.

I started out on this talk as a hydrobiologist. I wound up with some broad generalizations, viewing the world made from cells as a whole. May be I have ended up in a blind alley, but I think that theoretically minded persons could squeeze more out of these relations than I have been able to.

Returning to less lofty levels, I suggest that the factual basis for these generalizaticns deserves to be tested in studies with marine and aquatic

organisms and with representatives of the animal life in the soil and in the bottom-materials from lakes and the sea. The life of the marine sands might prove particularly interesting because this is a variegate world of micro--animals, all the size of grains of sand. The curves shown predict a standard range of metabolism for these organisms.

This excursion of a hydrobiologist into general biology should bring us back to the sea and to the hydrobiologist. When I did the work here reported I felt a great freedom in spite of war-time limitations, among them financial. One man surrounded by his many friends, the tiny creatures from the sea, each the center of its own world the same as he. A tiny room, a collecting net, homemade cheap instruments. I like to assist Dr. KLEKOWSKI in his propaganda for simple Cartesian diver methods for use in hydrobiology. A battery is now available (ZEUTHEN 1964, KLEKOWSKI 1967, 1968). They opened a world for me, the world of the small animals which can grow and evolve and keep energetic. Is this not a central issue when we speak of evolution of life in the sea? And a good one to study under the bastions of Hamlet's Kronborg.

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J. Phillipson

THE "BEST ESTIMATE" OF RESPIRATORY METABOLISM: ITS APPLICABILITY TO FIELD SITUATIONS*

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ABSTRACT

The "best estimate" of respiratory metabolism is an expression of mean energy loss per unit weight per unit time as calculated from laboratory measurement on all life stages of the species studied. It is independent of population data, temperature fluctuations, and generation time when this exceeds one year. Laboratory measurements of respiration, converted to mean annual field temperature, are used in conjuction with mean annual biomass data. Comparisons are given of the results obtained from the "best estimate" method with more detailed analyses.

INTRODUCTION, AND HISTORICAL BACKGROUND

It is clear from discussion and published work (MacFadyen, 1967) that there is misunderstanding of the "best estimate" concept as used by Phillipson (1962, 1963, 1967). This paper reconsiders the concept, explains the calculation; and supports by analyses of data, both published and unpublished, the contention that the "best estimate" can be a reliable and, in the long term, time saving contribution to the estimation of annual respiratory expenditure by populations. The examples given include a log dwelling beetle, a freshwater odonatan, a soil dwelling enchytraeid, and a litter dwelling phalangiid.

The term "best estimate" was first used by the present author (Phillipson, 1962) in referring to the mean calorie expenditure per unit weight per unit time of a given species as calculated from laboratory respiration data covering all life stages. It was suggested that the "best estimate" could be used in conjunction with biomass data to estimate a population's annual energy loss due to respiration. This approach was adopted by Phillipson (1963) to evaluate the annual respiratory metabolism of a species population where the age composition was not known and only biomass data were available.

In a later paper Phillipson and Watson (1965) stated: "because of the variability of respiratory rate with size, breeding, condition and season, it is clear that all the year round studies of all life stages of a chosen species are essential if one is to even approach an accurate estimate of the annual respiratory metabolism of a species population. As studies such as these are made it will be possible to arrive at a "best estimate" of respiratory energy loss per unit wt. over the whole life cycle. The "best estimate" should thus prove valuable in energy flow studies not only in allowing use to be made of past population studies where only biomass data are available, but also in future studies on energy flow, where it will obviate detailed observations on the life stage composition of the species population under consideration".

* This paper was delivered at the symposium "Bioenergetics of Aquatic Animals" held in Warsaw to celebrate the 50th Anniversary of the Nencki Institute.

More recently PHILLIPSON (1967) extended the concept of "best estimate" to parameters other than respiration in the ecoenergetic equations:

$$C = A+F$$

$$A = R+P$$

where: C — consumption, A — assimilation, F — faeces, R — respiration, P — production.

However, the present paper is restricted to consideration of the "best estimate" of respiration.

THE "BEST ESTIMATE" AND ITS CALCULATION

The "best estimate" of respiratory metabolism is an expression of mean energy loss per unit wt. per unit time as calculated from laboratory measurements on a l l life stages of a given species. Its calculation is independent of field population data; fluctuations in field temperatures; and generation time when this exceeds one year. Calculation of the "best estimate" depends upon 1) a reliable respirometer, preferably continuously recording, which is operated at a constant temperature, and 2) oxygen consumption determinations on all life stages of the species being studied. The phrase "all life stages" can be interpreted as stadia or instars when these can be separated, or size classes of a p p r o p r i a t e magnitude when they cannot. Table I shows one example of the "best estimate" using instars and one using appropriate size classes. It should be noted that in the case of *Melanotus rufipes* Hbst. the "best estimate" was calculated for a temperature of 15°C, a temperature some 5°C higher than the annual mean temperature of its normal habitat; whereas

Table I. Two examples of "best estimate" calculation, one according to instars and the other according to size categories

Instar	*Melanotus rufipes* Hbst.		*Pyrrhosoma nymphula* (Sulz.)		
	Mean live wt. (mg)	μl O_2/ind.·24 hr at 15°C	Size class (mg)	Mean live wt. ($mg \cdot 10^{-2}$)	$\mu l \cdot 10^{-2}$/ind.·hr at 8.5°C
1	0.16	22.80	0.0—0.5	21.3	0.1754
2	0.29	29.52	0.5—1.0	78.9	2.0400
3	0.53	38.40	1.1—5.0	255.1	2.3360
4	0.95	49.92	5.1—10.0	789.5	26.6100
5	1.50	56.88	10.1—20.0	1574.0	28.8100
6	2.10	56.40	20.1—40.0	3065.0	31.1100
7	3.10	52.08	40.1—60.0	4749.1	327.3000
8	4.90	68.16	60.0	6060.0	673.4000
9	7.10	71.52			
10	14.00	97.44			
11	20.50	103.44			
12	24.30	124.08			
13	59.20	156.24			
14	88.50	169.92			
15	119.80	172.56			
Total	356.93	1,269.36	total	16,592.9	1,091.7814

Best estimate = $\dfrac{1,269.36}{356.93}$ = 3.56 μl O_2/mg·24 hr at 15°C

best estimate = $\dfrac{1,091.7814}{16,592.9}$ = $65.9 \cdot 10^{-3}$ μl O_2/mg·hr at 8.5°C

that of *Pyrrhosoma nymphula* (Sulz) was measured at 10°C and corrected to the annual mean temperature of its habitat using the logarithmic regression of respiration versus weight: $y = 0.867x - 0.832$ where y equals log R (in $\mu l \cdot 100$/larva·hr), and x equals log live wt. (in mg·100). In both instances annual mean field temperatures were obtained according to the method of BERTHET (1960).

When the "best estimate" is to be used in conjunction with biomass data it is essential that it be calculated for the annual mean temperature of the habitat. Table II gives the necessary correction factors for *M. rufipes* larvae at

Table II. *Melanotus rufipes*: temperature correction factors expressed as a percentage of the respiratory rate at 15°C

	Temperature (°C)			
	5	10	15	20
$\mu l \ O_2$/mg · hr	0.06	0.08	0.13	0.20
Per cent of uptake of O_2 at 15°C	46	61	100	131

5, 10, 15 and 20°C. The correction factors are expressed as a percentage of respiration at 15°C, and it was calculated that the "best estimate" for *M. rufipes* at the annual mean temperature of its habitat (9.7°C) is equivalent to 2.17 $\mu l \ O_2$/mg live wt.·24hr. A "best estimate" for the phalangiid *Oligolophus tridens* (C. L. Koch) at 16°C was calculated according to the instar method by PHILLIPSON (1962) as 25.554 mm³ O_2/mg live wt.·24hr. For *P. nymphula* the size category method gave rise to a "best estimate" of $65.9 \cdot 10^{-3}$ $\mu l \ O_2$/mg live wt.·hr at 8.5°C. By applying the size category method to the respiratory rate curve given by NIELSEN (1961) for the enchytraeid *Fridericia* at 20°C it was possible, knowing *Fridericia* spp. respiration to approximate Krogh's curve, to calculate a "best estimate" of $1.55 \cdot 10^{-2}$ $\mu l \ O_2$/μg N·hr at the annual mean temperature of the habitat (9.4°C).

It is clear that biological units such as instars will give equal weighting to each life stage in the calculation of the "best estimate", this is not necessarily the case when arbitrary size classes are used in lieu of life stages. In order to avoid overweighting in the case of particular life stages, size categories should not be selected on an arithmetic scale but on a scale approximating a sigmoid curve resembling the growth curve. This was done in the case of *P. nymphula* and Fridericia.

Given "best estimates" of respiratory loss based on laboratory determinations, and a knowledge of annual mean temperatures in the field, it is possible to estimate with reasonable accuracy the annual respiratory loss from mean annual biomass data. No measure of biomass fluctuations or age composition of the population is necessary.

ANNUAL RESPIRATORY METABOLISM OF *FRIDERICIA* SPP., *M. RUFIPES* AND *P. NYMPHULA*

The use of the "best estimate" in conjunction with mean annual biomass data to estimate annual respiratory loss from a population can be illustrated by reference to the organisms already mentioned.

Table III shows the biomass estimates from which mean annual biomass was calculated for *Fridericia* spp., *M. rufipes* and *P. nymphula*. In the case of Fridericia the mean monthly figures were read from the graph given for Station 1 by NIELSEN (1961); the mean annual biomass thus calculated (2.97 g live wt./m²) was equal to the weight tabulated by him (2.97 g live wt./m²). Annual mean biomasses of Fridericia quoted by NIELSEN (1961) for Stations 4 and 18 were 3.03 and 10.50 g live wt./m² respectively. The annual mean biomass of *M. rufipes* was 1966.3 mg live wt./100 l of log, and those of *P. nymphula* 1169.7 mg live wt./m² (1966–67) and 1567.7 mg live wt./m² (1967–1968).

NIELSEN (1961) gave the nitrogen content of *Fridericia* spp. as 2.23 ± 0.04

Table III. Biomass figures from which mean annual biomass was calculated for Fridericia, Melanotus and Pyrrhosoma. Mean monthly temperatures of the habitat are also given

Fridericia spp. (Station 1, NIELSEN 1961)			*Melanotus rufipes*		
month	mean temp. °C	biomass (g live wt./m²)	month	mean temp. °C	biomass (mg live wt./100 l of log)
1966			1966		
October	9.9	2.9	June	11.40	552.4
November	2.5	3.2	July	12.24	3928.8
December	3.3	4.0	August	12.13	1465.2
1967			September	12.19	3314.4
January	1.5	4.0	October	10.00	4013.5
February	0.2	4.1	November	7.21	—
March	1.4	4.4	December	5.12	1124.7
April	6.0	5.5	1967		
May	12.6	3.2	January	5.16	625.8
June	18.1	0.7	February	6.67	877.7
July	20.3	0.8	March	7.18	1983.4
August	18.6	1.0	April	7.10	1692.9
September	14.6	1.9	May	10.03	2050.8
Mean	9.4	2.97	Mean	9.7	1966.3
Pyrrhosoma nymphula 1966—1967			*Pyrrhosoma nymphula* 1967—1968		
month	mean temp. °C	biomass (mg live wt./m²)	month	mean temp. °C	biomass (mg live wt./m²)
1966			1967		
July	15.04	1435.2	July	15.30	643.2
August	14.44	1937.1	August	14.72	1162.8
September	11.95	2531.0	September	12.31	1994.4
October	9.55	2375.9	October	8.35	2523.3
November	6.72	1681.6	November	4.83	2422.1
December	3.61	1203.6	December	2.86	2154.1
1967			1968		
January	2.82	794.3	January	2.84	1876.9
February	4.91	600.1	February	3.17	1700.9
March	6.17	447.0	March	5.58	1555.0
April	6.44	363.7	April	7.35	1056.7
May	9.93	328.6	May	10.53	1492.3
June	13.52	337.7	June	14.34	231.0
Mean	8.76	1169.7	Mean	8.52	1567.7

(SD) per cent of live wt., thus the "best estimate" of $1.55 \cdot 10^{-2}$ µl O_2/µg N·hr can be expressed as $1.55 \cdot 10^{-2}$ µl O_2/44.8 µg live wt.·hr or 3.03 l O_2/g live wt.· ·yr. (Compare with NIELSEN's mean annual respiration figures of 2.4, 3.3 and 3.1 l O_2/g live wt.·yr for Station's 1, 4, and 18 respectively). "Best estimates" of the remaining three species have already been given as volume of O_2/unit wt.·unit time.

Mean annual biomass when multiplied by the "best estimate" of respiration, converted to an annual basis at the mean annual field temperature, gives an estimate of annual respiratory loss by the population. Table IV

Table IV. Annual respiratory loss of six populations when estimated as the product of the "best estimate" at the annual mean temperature and the mean annual biomass

Population	"Best estimate" at mean temp. of habitat (µl/mg·yr)	Mean annual biomass (mg live wt.)	Estimated annual respiratory loss	
			ml O_2	kcal
Fridericia Stn. 1	3030.0	2970.0/m²	8918.9/m²	43.024/m²
Fridericia Stn. 4	3030.0	3030.0/m²	9180.9/m²	44.294/m²
Fridericia Stn. 18	3030.0	10500.0/m²	31850.0/m²	153.763/m²
M. rufipes (1966—67)	792.1	1966.3/100 l.	1557.5/100 l.	7.515/100 l.
P. nymphula (1966—67	577.3	1169.7/m²	675.3/m²	3.258/m²
P. nymphula (1967—68)	577.3	1567.7/m²	805.0/m²	3.884/m²

shows the estimates for three populations of Fridericia, one of *M. rufipes* and a population of *P. nymphula* in two consecutive years. In the final column an oxycalorific equivalent of 4.825 kcal/l was used to convert oxygen volumes to kcals. The accuracy of the estimates for the three Fridericia populations can be checked against NIELSEN's (1961) published figures. The annual respiratory energy loss by *M. rufipes* was calculated (making corrections for field temperature fluctuations) from the data given in Tables I–III, and amo-

Table V. A comparison of estimates of annual respiration losses by six populations

Population	Annual respiratory energy loss using "best estimate"		Annual respiratory energy loss allowing for field temp. fluctuations and size class composition		Percentage error of "best estimate"
	ml O_2	kcal	ml O_2	kcal	
Fridericia Stn. 1 per m²	8,918.9	43.024	7,000.0	33.964	+21.1
Fridericia Stn. 4 per m²	9,180.9	44.294	10,000.0	48.520	—9.5
Fridericia Stn. 18 per m²	31,850.0	153.763	32,000.0	155.264	—1.0
M. rufipes (1966—67) per 100 l.	1,557.5	7.515	1,445.7	7.025	+3.5
P. nymphula (1966—67) per m²	675.3	3.258	659.5	3.200	+1.8
P. nymphula (1967—68) per m²	805.0	3.884	766.7	3.700	+4.7

3*

unted to 7.025 kcal/100 l·yr. With *P. nymphula* detailed calculations, which were made by J. H. Lawton, equalled 3.2 kcal/m² (1966–1967), and 3.7 kcal/m² (1967–1968). Table V shows the comparative figures for all six populations and an indication of the degree of accuracy obtained by the "best estimate" method. It is of interest to note that the more detailed calculations with Fridericia and *M. rufipes,* although including corrections for temperature fluctuations and size class composition of the population, did not allow for the respiration of animals that died between sampling intervals. The calculations with *P. nymphula* did include such allowance. The possibility that the "best estimate" method accurately reflects total respiratory loss by a population is here considered more fully by reference to the litter dwelling phalangiid *Oligolophus tridens.*

ANNUAL RESPIRATORY METABOLISM OF *OLIGOLOPHUS TRIDENS*

A "best estimate" at 16°C for *O. tridens* was given by Phillipson (1962) as 25.554 mm³ O_2/mg live wt.·24 hr. Table VI gives detailed data on dry wt. biomass/m², and from these an annual mean biomass of 7.407 mg dry wt./m² was calculated. The mean water content of *O. tridens* is 79.9% of total live

Table VI. Dry wt. biomass/m² of *O. tridens* in Great High Wood from September/October 1958 to November 1959. A point represents zero

Date of sampling	Dry wt. (mg/m²)								
	eggs	II	III	IV	V	VI	VII♂	VII♀	Mean wt./ind.
1958									
Sept./Oct.	55.777	—	—	—	—	—	—	—	0.045
1959									
28 May	—	0.910		.	.	.	.	.	0.065
13 June	.	0.910	0.760	.	.	.	.	.	0.076
30 June	.	.	0.190	2.665	.	.	.	.	0.190
15 July	.	.	0.095	2.460	0.734	.	.	.	0.219
4 August	.	.	.	.	4.771	.	.	.	0.367
20 August	.	.	.	.	.	10.350	1.900	.	1.225
2 Sept.	.	.	.	.	.	3.450	9.500	13.720	2.223
16 Sept.	—	.	.	.	.	.	20.900	10.290	2.228
22 Sept.	—	.	.	.	.	.	3.800	20.580	3.048
11 Oct.	—	.	.	.	.	.	1.900	6.860	2.920
31 Oct.	—	.	.	.	.	.	.	3.430	3.430
11 Nov.	—	.	.	.	.	.	.	3.430	3.430

wt., thus the dry wt. biomass/m² is equivalent to an annual mean biomass of 37.034 mg live wt./m². Animals were present in the field from May to November (213 days) and using the "best estimate" for this period of time multiplied by 37.034 mg live wt./m² the annual respiratory metabolism was estimated at 201.576 ml O_2/m² (968 cal/m²·hr).

A more detailed calculation was made using the figures for population density shown in Table VII in conjunction with the daily respiratory rates of different instars given in Phillipson (1962). Because of the difficulty of calculating the proportion of any one instar dying to that moulting into sub-

Table VII. The number of *O. tridens*/m² in Great High Wood during 1959. A point represents zero

Date of sampling	II	III	IV	V	VI	VII ♂	VII ♀
24 April		.	.	.	.	.	.
11 May	.	.	.	.	.	.	.
28 May	14	.	.	.	.	.	.
13 June	14	8	.	.	.	.	.
30 June	.	2	13	.	.	.	.
15 July	.	1	12	2	.	.	.
4 August	.	.	.	13	.	.	.
20 August	.	.	.	.	9	1	.
2 September	.	.	.	.	3	5	4
16 September	.	.	.	.	.	11	3
22 September	.	.	.	.	.	2	6
11 October	.	.	.	.	.	1	2
31 October	.	.	.	.	.	.	1
11 November	.	.	.	.	.	.	1
5 December	.	.	.	.	.	.	.

sequent instars during the interval between sampling dates, a number of assumptions were necessary. It was assumed that:

1) Instars appearing for the first time at t_1 had moulted midway in the period t_0–t_1. Respiration of these forms was calculated as:

$$n_t \cdot \frac{1}{2} \cdot r_{t_0-t_1}$$

where: n_i is the number of a single instar present at time t_1, $r_{t_0-t_1}$ is the total respiration of a single individual of any one instar during the interval between sampling dates, and $\frac{1}{2}$ is based on the assumption that moulting occurred midway in the interval between sampling dates.

2) The numbers of each instar present at time t_1, when that instar also occurred at time t_0, had been present over the whole period between sampling dates. Respiration of these forms was calculated as: $n_t \cdot r_{0-t_1}$.

3) Given a constant mortality rate and that equal numbers of each instar present at time t_1 died in the interval between sampling dates then respiration of the animals that did die could be calculated as:

$$\frac{\Delta N}{\Delta t} \cdot \frac{1}{2} \cdot \frac{\sum r_{t_0-t_1}}{\sum n_t},$$

where: $\frac{\Delta N}{\Delta t}$ is the number of individuals dying in the interval between sampling dates, $\frac{\sum r_{t_0-t_1}}{\sum n_t}$ is the mean respiration per individual, irrespective of life stage, during the interval between sampling dates, and $\frac{1}{2}$ is based on a constant mortality rate. The results are shown in Table VIII and it is clear that total annual respiratory metabolism amounted to 199.415 ml O_2/m² (957 cal/m²·yr), a figure within 2% of that predicted by the "best estimate" method (968 cal/m²·yr).

Table VIII. Respiration/m² by *O. tridens* in 1959. The conversion figures are from PHILLIPSON (1962), although those in brackets were estimated. A point represents zero

Conversion figures (μlO₂/ind · 24 hr)	Instar						
	II	III	IV	V	VI	VII♂	VII♀
	(14.63)	(29.26)	43.89	62.42	218.57	Aug. 189.45 Sep. (208.16) Oct. 226.87	Aug. 344.74 Sep. 253.27 Oct. (300.43) Nov. 347.59

Respiration (μl O₂/m²); Instar

Date of sampling 1959	II	III	IV	V	VI	VII♂	VII♀	Animals that died	Total
11 May–28 May	1740.97	.	.	.	.	.	.	—	1740.97
28 May–13 June	3277.12	1872.64	.	.	.	.	.	—	5149.76
13 June–30 June	.	994.84	4849.85	.	.	.	.	2176.51	8021.20
30 June–15 July	.	468.16	8426.88	998.72	.	.	.	0.00	9893.76
15 July–4 August	.	.	.	16229.20	.	.	.	1248.40	17477.60
4 Aug.–20 Aug.	.	.	.	.	15737.04	1515.60	.	4896.24	22148.88
20 Aug.–2 Sept.	.	.	.	.	8524.23	12314.25	8963.24	0.00	29801.72
2 Sept.–16 Sept.	.	.	.	.	.	32056.64	10637.34	0.00	42693.98
16 Sept.–22 Sept.	.	.	.	.	.	2497.92	9117.72	4152.96	15768.60
22 Sept.–11 Oct.	.	.	.	.	.	4310.53	11416.34	12523.47	28250.34
11 Oct.–31 Oct.	.	.	.	.	.	.	5708.17	2854.09	8562.26
31 Oct.–11 Nov.	.	.	.	.	.	.	6604.21	0.00	6604.21
11 Nov.–5 Dec.	.	.	.	.	.	.	.	3302.11	3302.11
Total annual respiration									199415.39

DISCUSSION

In five out of the seven cases discussed the "best estimate" method of calculating annual respiratory metabolism provided estimates within 5% of those obtained by detailed analyses requiring a knowledge of field temperature fluctuations, size class composition of the population; and in the cases of *P. nymphula* and *O. tridens,* mortality also. With *M. rufipes* the "best estimate" of annual respiration was within 10% of the detailed study. In six cases out of seven it is considered reasonable to claim high accuracy for the "best estimate" method of estimating annual respiratory losses by populations. Further support may be found in HINTON (1968) who used four different methods of calculating annual respiratory loss by a population of the spittle bug *Neophilaenus lineatus* L.; that derived by the "best estimate" method was within 2% of the detailed estimate.

The reasons why the "best estimate" methods gives results so near to those obtained by more sophisticated methods are not clear; however, tentative explanations can be put forward. Because the "best estimate" of respiration gives equal weighting to a l l life stages and results in a mean value for oxygen consumption per unit wt. and per unit time by an "average" animal, it is independent of generation time and the size class structure of the population. The "best estimate" is not equivalent therefore to NIELSEN'S (1961) mean annual respiration as stated by MACFADYEN (1967). Clearly, approximation to an "average" animal is most likely when the size class composition of the population is stable throughout the year. This situation will more readily arise when the life cycle occupies several years (e.g. *M. rufipes*) and/or recruitment to the population is continuous over most of the year (e.g. Fridericia). Approximation should be poorest when the life cycle is short and recruitment occurs over a very short period of time (e.g. *P. nymphula* and *O. tridens*). In the latter case the high respiratory rate per unit wt. of young individuals will affect markedly weekly, or monthly, estimates of respiratory loss; if applied to such short time periods the "best estimate" would lead to an underestimate. However, the duration of young stages as members of the population is short and it can be argued that their contribution to respiratory loss on an annual basis is insignificant; this certainly appears to be so with *P. nymphula* and *O. tridens*. The "best estimate" of respiration calculated from all life stages should not therefore be applied to periods shorter than a generation time unless this exceeds one year, in which case estimates of annual respiratory loss can be made. Besides the problem of size class composition of the population there remains the problem of temperature fluctuations. If an animal shows acclimation to temperature, i.e. retains a more or less constant oxygen consumption irrespective of temperature, then corrections for temperature fluctuations are unnecessary. In many cases, however, poikilotherm respiratory rates are influenced by temperature so that corrections for temperature fluctuations are deemed necessary (MACFADYEN 1967). Annual temperature fluctuations in a given habitat usually follow a gradual curve and imposition of the arithmetic mean on such a curve will give rise to equal areas above and below the curve. It is clear that the use of the "best estimate" at the annual mean temperature of the habitat will underestimate respiratory loss in certain months and overestimate in others, yet on an annual, or generation time basis, the errors will cancel out. It is again obvious

that the "best estimate" should not be employed for periods of time shorter than a generation time, or less than one year when generation time is greater than twelve months. Additional support for the argument that corrections for field temperature fluctuations are unnecessary, providing the annual mean temperature is known, is provided by HEALEY (1967) who states in the discussion following his paper on *Onychiurus procampatus* Gisin "... if population metabolism of *O. procampatus* is calculated using in each month, not the true observed soil temperature, but the annual (arithmetic) mean temperature of 9.3°C, total oxygen consumption for the year comes to 537 ml O_2/m^2, i.e. only 2% less than the total of 548 ml O_2/m^2 obtained using full (logarithmic) temperature correction".

On the basis of the evidence currently available it is the present author's opinion that the "best estimate" method of estimating annual respiration has great potential, although the 21% discrepancy between the two estimates for Fridericia at Station 1 remain unexplained as yet.

If the arguments put forward in this paper prove acceptable to workers interested in comparing annual respiration losses of different populations it is clear that detailed, and relatively short term, laboratory studies to elucidate "best estimates" of respiration will reduce the number of population parameter measurements normally required for the estimation of population metabolism. Indeed the only necessary field measurements would be annual mean biomass and annual mean temperature of the habitat. Whilst it is true that short term variation in energy flow cannot be estimated by this method, its advantages are obvious. Given "best estimates" past biomass data can be utilized for comparative purposes: direct comparisons of species populations, from a variety of habitats within the same time period are within the capabilities of a single worker; and an invaluable, and previously unavailable, opportunity is offered to small groups of workers for the elucidation of the relative roles of different species populations in a single habitat, within any one years.

Finally, it appears that the regressions for various populations of log production versus log respiration given by ENGELMANN (1966) are valid; given annual respiration of a population by the "best estimate" method it should prove possible to estimate the annual production of that population.

SUMMARY

1. The "best estimate" of respiratory metabolism is an expression of mean energy loss per unit wt. per unit time as calculated from laboratory measurements on all life stages of the species studied. It is independent of population data, temperature fluctuations, and generation time when this exceeds one year.
2. The laboratory measurements are made at a constant temperature on identifiable life stages e.g. instars, or size categories chosen at equal intervals along the horizontal axis of a sigmoid curve resembling the growth curve of the species.
3. When converted to mean annual field temperature the "best estimate" can be used in conjunction with mean annual biomass data to give reliable estimates of annual respiratory metabolism. In six of the seven populations chosen as examples, the "best estimate" method gave results within 10% of estimates made by more detailed analyses requiring the measurement of several population parameters, and also correction for field temperature fluctuations.
4. Although short term variations in energy flow cannot be accurately calculated by the "best estimate" method, it is felt that this method provides hitherto unavailable opportunities for comparing with considerable accuracy the metabolic role of species populations in one or more habitats within the same time period.

Acknowledgements

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SOME REMARKS ON THE NECESSITIES AND PROSPECTS OF THE STUDIES ON BIOLOGICAL PRODUCTION OF FRESHWATER ECOSYSTEMS

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ABSTRACT

The prospects, necessities, and difficulties when studying the production of freshwater ecosystems were analysed on the grounds of exemplary data from the Mazurian Lakes. Following trends in production investigations were distinguished: estimation of the production of species and groups, estimation of the production efficiences of neighbouring trophic levels (energy balances of species and entire communities). Using the material from several lakes of various types presented were: differences in biomass and gross primary production (and their course in the annual cycle) and nannoplankton participation in production, biomass and production of zooplankton and zoobenthos and their various components, food composition and the effect of food concentration on zooplankton production, the influence of competition relations of benthos on its abundance and feeding, intensity and the course of destruction in pelagial and profundal (on the grounds of a comparison of primary production and the amount of sedimentating tripton).

Learning about the production regularity is very important both from the theoretical and practical side. The theoretical side is important because it provides the grounds to understand the functioning of biocenosis and ecosystems and characterizes them more precisely than it is possible in the categories of number and biomass of organisms. The practical approach is justified by the fact that these regularities of organism production decide about all effects of organism development in water we are concerned with, e.g. water purity, sewage treatment, clogging of the filtration system in power plants, fish production and so on.

Studies on production are not a new trend in the research field but an attempt of a more detailed quantitative approach to phenomena in nature. This may, however, lead to completely new conclusions with respect to the estimation of number or biomass.

The purpose of studying the production is the same as it has been always in ecological and hydrobiological fields — namely to comprehend the functioning of ecosystems, but the method used is more precise.

Reflecting upon the present situation in the field of production investiga-

tions of freshwater ecosystems few examples taken from the research on the production of Mazurian Lakes may be used.

Following trends of production investigations may be distinguished:

1) estimation of the production of respective species or groups of organisms. Still little is known about the production intensity — the dependences between production and biomass and their differentiation in various situations.

2) analyses of ecological efficiences of neighbouring trophic levels:

a) energy balances of respective species analysed almost as a rule in laboratory conditions;

b) elements of energy balances of entire communities or fragments of ecosystem, e.g. pelagic plankton, periphyton, benthos etc. Sometimes only trophological investigations and sometimes widened by investigations of other connections and interactions.

3) energy balances of ecosystems:

a) entry and exit (primary production and on one hand allochtonous substance and on the other sedimentating tripton and products removed from the water body);

b) detailed diagram of energy flow. There are several such papers — LINDEMAN (1942); ODUM (1957); TEAL (1957); DAVIS and WARREN (1965); SITARAMAIA (1967); WINBERG (1970) and others. Recently KCZLOVSKY (1968) compiled the results of these 5 papers.

One of the most essential advantage of the production approach is the possibility of checking the obtained quantitative results. E.g. if the animal consumes the C amount of food, this amount must be equal to the sum of animal's biomass increase, its metabolism expenditures and faeces. It is the same in case of ecosystem or trophic level — the sum of organic substance supplied from the outside must be equal to the sum of metabolic expenditures and the products leaving the given links.

In order to be sure of the accuracy and comparability of data, and also to be able to draw diagrams of energy balances it is necessary to have absolute data not the indicating ones. Obtaining the absolute data is indispensable in production investigations. Much has been already done to fulfill this condition but it is not everything yet.

The research on production carried so far, and in that the mentioned attempts to characterize the energy balances, explained several matters but also brought out the difficulties and matters, which should be solved, and of which nobody was aware of before starting the research work on production.

At present it is known that the field production investigations do not give absolute estimations, but these estimations are definitely better than number and biomass. And so e.g. only production approach gives the possibility of comparing pelagial and littoral and the participation of organisms of each of these habitats in the total primary production of the water body.

Despite several methodical limitations of the reliability of results in tripton production these data supply valuable general information on the functioning of lake ecosystem (the above mentioned analysis of "entry and exit" of ecosystem p. 3, item 3a). E.g. for Mikołajskie Lake on the grounds of a comparison of data on primary production of pelagial and sedimentation of tripton (Fig. 1, acc. to ŁAWACZ 1969, and unpublished data) it was possible to estimate the destruction process of organic substance during the season

Fig. 1. Changes in primary production and sedimentation of tripton. Lake Mikołajskie (acc. to ŁAWACZ 1969). 1 — gross primary production, 2 — tripton (16 m), 3 — tripton (10 m)
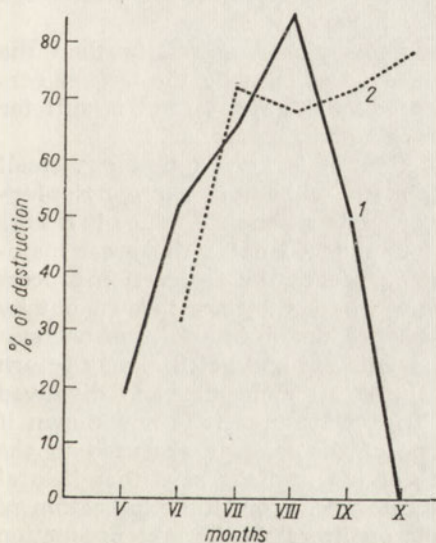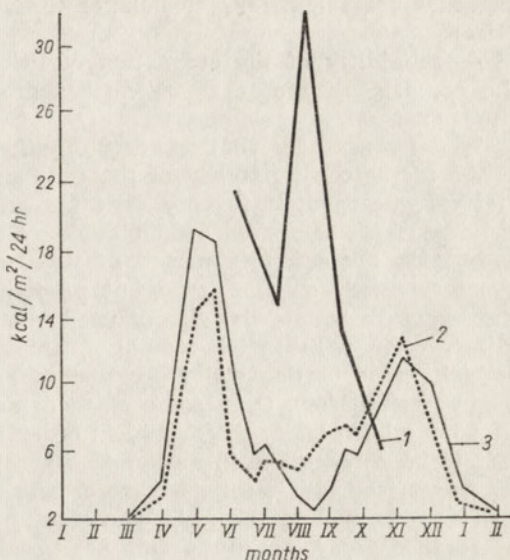

Fig. 2. Changes of the destruction intensity. Lake Mikołajskie (acc. to ŁAWACZ 1969). 1 — gross primary production minus the sedimentary tripton, 2 — on the grounds of oxygen consumption in dark and light bottles

(Fig. 2, acc. to the unpublished material of ŁAWACZ) and introduce a hypothesis about the important role of organic substance dissolved in water, and especially in the period of autumn circulation. Comparing the amount of tripton sedimentating during a year with the amount of sediments in one year (calculated by ŁAWACZ, unpublished data, acc. to WIĘCKOWSKI 1966) allowed to assess that only 3-7% of sedimentating tripton remains in bottom sediments and the rest returns to the lake circulation.

In connection with the attempts to compare various links and communities

in water ecosystems and to balance the ecosystem production, two problems
arise:

— reliability of the estimation of primary production, and by the same
the comparability of data of various groups of producers and in different
situations;

— the sense of global treating of different kinds of primary production.

As far as the reliability of the estimation of primary production of pela-
gial is concerned, it is very well known that the absolute values are not
obtained. This is proved even though by not coinciding results of production
estimation for a longer period of time (e.g. 24 hr) and summed results of
shorter periods of time, different production results depending on the time
the exposure began, the size of used vessels, influence of metal (when sam-
pling water with metal samplers), changes of light conditions during the
exposition of bottles etc. More doubts and limitations could be mentioned
(Oporowska 1966). Only some of them are mentioned here, especially those
that have been lately discovered in order to point out how much there is still
left to be done to obtain authorative absolute results.

Apart from other things there are no completely precise data on net pri-
mary production in the field available and this is a base for the production
of further ecosystem links and not gross primary production. Therefore it
would be advisable to confront various methods of estimation of net produc-
tion, e.g. methods of biomass and C_{14} increases, even during the first stage
in laboratory conditions, or during the water blooms.

Production estimation in its present stage is closer to reality than the
estimation of number or biomass, which is proved at least by the lack of cor-
relation of phytoplankton biomass and its production (Fig. 3), but is still far
from being perfect.

The problem of summing up the production. It is known that e.g. small
planktonic algae are directly used by consumers, while the macrophytoplan-
kton and the majority of macrophytes only after destruction. And, as it results
from the investigations of E. Pieczyńska (unpublished data), the great majo-
rity of produced mass of littoral macrophytes undergo the destruction process
not in the lake but in the bank littoral zone, where they are thrown out by
the waves. At a higher water level part of this production in a form of bacteria
bodies, animals developing on the decaying vegetation and detritus may return
to the lake; at a low water level — only the small molecular and dissolved
destruction products return mainly to the lake. Of course it is not known if
these products penetrate to the central zone of the lake or are used in the
littoral. Straskraba (1963) on the grounds of his findings says that littoral
uses for production more of not uniform substances. From the explanation of
these problems it would depend how the role of littoral in the lake production
would be treated — whether as a co-producer (beside pelagial communities)
in the entire lake or as a consumer of pelagial production.

Also the problem whether the primary production may be treated as
a sum is actual in case of pelagial as there can be distinguished production
directly available for plankton consumers and that unavailable mainly be-
cause of the size of cells and "digestibility" of cellular walls. The data from
3 Mazurian Lakes may be an example of the variation of primary produc-
tion from the standpoint of its utilization in ecosystem and within that by
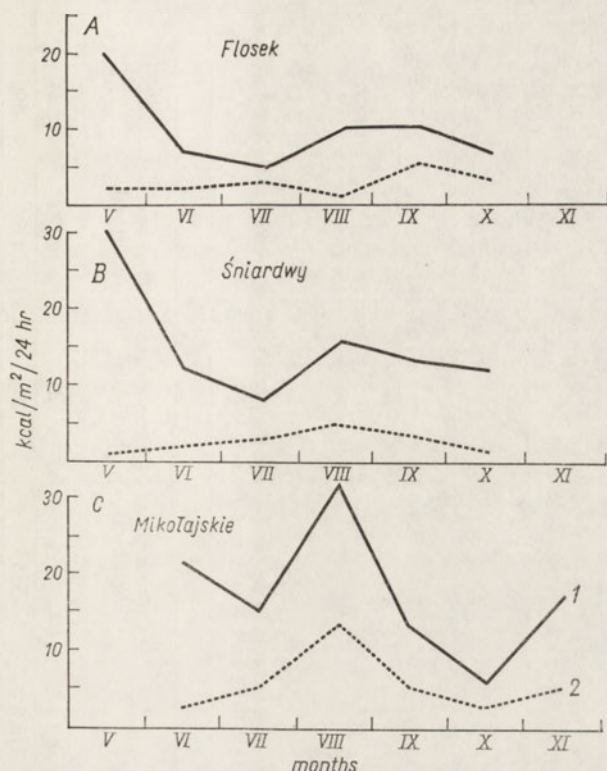consumers. Respective lakes differ greatly from the point of mean annual

Fig. 3. Variation of biomass and phytoplankton production in 3 lakes (acc. to HILLBRICHT-ILKOWSKA and SPODNIEWSKA 1969). A — Lake Flosek, B — Lake Śniardwy, C — Lake Mikołajskie. 1 — gross production kcal/m²/24hrs, 2 — biomass mg/l

values, nannoplankton biomass, and so of food directly available for consumers, and also its participation in production. The great differences between the lakes and also within the lake are seen, when the range of fluctuations of some production indicators, biomass, relative activity and participation of nannoplankton in production (Table I) are taken into consideration. Another example may be the dependence of qualitative composition of phytoplankton on its production — the greater is the participation of blue-green algae the lower is the production efficiency (Fig. 4, acc. to HILLBRICHT-ILKOWSKA and SPODNIEWSKA 1969).

All these data are a sufficient proof that there is a necessity of detail analyses instead of being limited to a summary characteristic of production in order to determine the role of respective components and quantitative and qualitative investigations joint.

Examples of differences between primary production and biomass of producers have been already given. There is a great differentiation also within the range of secondary production (Table II). The proportion of production to biomass in epilimnion in case of rotifers exceeds in one season 40.0. Benthos production in Lake Tałtowisko per surface unit in sublittoral is even higher

Table I. Net primary production of pelagial and indicators of its intensity. Big numbers — mean values for the season, small — range of fluctuations during the season (acc. to HILLBRICHT-ILKOWSKA and SPODNIEWSKA 1969)

Lake	Production kcal/m²/24 hr	Biomass mg/l		Relative activity		Indication of nannoplankton participation in production — %	% of utilization of solar energy
		of the entire phytoplankton	of the entire nannoplankton	of the entire phytoplankton	of the entire nannoplankton		
Mikołajskie	16.8 5.7–31.7	4.7 1.3–12.9	1.2 0.7–1.5	1.2 0.8–2.5	3.8 2.1–5.7	62 23–234*	0.48 0.32–0.78
Śniardwy	14.0 7.8–30.7	2.1 0.2–5.2	0.6 0.1–1.3	2.2 1.0–10.6	7.3 3.3–19.6	79 63–102	0.40 0.17–0.91
Flosek	8.7 5.2–20.2	1.7 0.4–4.6	2.5 0.9–6.2	0.9 0.3–3.4	1.1 0.4–2.6	79 49–147	0.24 0.12–0.59

* values higher than 100% are of course relative, not absolute ones, due to method used.

Table II. Comparative data of the intensity of secondary production of various components (data per 1 m² for the period of one year) Taltowisko Lake (acc. to HILLBRICHT-ILKOWSKA and WĘGLEŃSKA 1970, and KAJAK and RYBAK 1966)

	Plankton					Benthos			
	Rotatoria	Cladocera	Diaptomidae	Cyclopidae	jointly	Chironomidae sublittoral	Chironomidae profundal	Dreissena sublittoral	jointly sublittoral benthos*
B	1.3	4.7	0.8	1.4	8.3	2.3	4	12.2	43
P	56	114	13.2	25.8	212.6	335	20	4.6	590
P/B	43	24.3	16.3	18.4	25.6	14.6	5	0.4	13.7

B — biomass, P — production in gramms of wet wt./m².
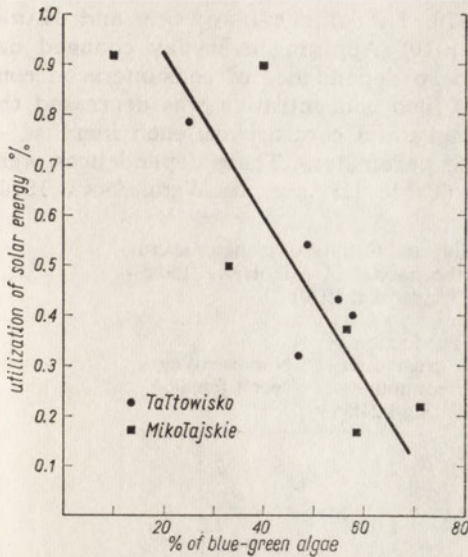* taking into consideration others — Oligochaeta, Gammaridae, Hirudinea, others Insecta, microbenthos.

Fig. 4. Utilization of solar energy in production and its dependence on the participation of blue-green algae in phytoplankton biomass (acc. to Hil-lbricht-Ilkowska and Spodniew-ska 1969)

than the plankton production. Differentiation of the proportion of production to biomass in respective groups and in classes of size and habitats is immense.

Of course the estimation of secondary production in the present stage of our knowledge is also an approximate value. Time of development and bio-mass increment of the given organism are the parameters necessary to cal-culate the secondary production. This is relatively simple in case of species having a short period of appearance of young generation, and very difficult for species having an extended period of reproduction and having all the time a differentiated size structure.

This problem is connected with the experimental investigations on pro-duction, including investigations of trophic dependences. There are many papers on the subject of rate and length of development among others (e.g. Gliwicz 1969 b, Węgleńska 1970). A frequent error is not taking into acco-unt the concentration and quality of food, which the organism has in nature. Almost as a rule food concentrations used in experiments are considerably greater than those in nature. Apart from that, the food applied in experi-ments is monotonous, often consisting of only one species, which the consumer rarely finds in nature.

Attention should be called to the fact that many conclusions concerning the food dependences are resulting from investigation which were carried out for a period too brief. Therefore one should be careful, when using the technique ^{14}C, which allows and even imposes a shorter period of investi-gations.

Meanwhile, food assimilation and the efficiency of growth of consumers on that food during a short (few hours or even shorter) period may be not representative at all; this food may be of no value for the development of organisms on a longer run (Smirnov, acc. to Telitcenko 1967). Irreplaceable from this point of view are the investigations on feeding on fully natural food in individual cultures and also in experiments with entire natural com-munities of species (Kajak et al. 1968, Kajak 1966, Węgleńska 1968,

GLIWICZ 1969, KAJAK and DUSOGE 1970, HILLBRICHT-ILKOWSKA and KARA-BIN 1970, KAJAK and RANKE-RYBICKA 1970). Applying everyday changed natural food, sampled from the lake a sharp dependence of consumers on concentration was observed. Each time the food concentration was decreased the fertility, growth etc. decreased accordingly and contrariwise each increase — caused an increase of the value of these parameters. These dependences were fully confirmed in field observations (Table III, acc. to WĘGLEŃSKA 1970).

Table III. Dependence of production and fertility of planktonic crus-taceans on food concentration in the habitat of Mikołajskie Lake—August (acc. to Węgleńska, 1970)

Period	Food concentration mg/l	Production of crustacean community mg/l 24hrs	Number of eggs per 1 female*
22.7—4.8	3.5	2.1	2.4 1.3—3.0
5.8—20.8	1.9	1.0	1.2 0.8—1.8
21.8—30.8	3.0	1.6	1.9 1.2—2.2

* averagely for the 5 dominant species (small numbers at the bottom) the range of fluctuations for respective species.

The differences "in minus" in the lake were about 10% in the period of good food conditions and some 30% when they were worse. A sharp dependence on the amount of food was observed in benthos experiments — each increase of the number of consumers caused a decrease of the amount of food in habitat and a decrease of the amount of food consumed. In turn each increase of the amount of food stimulated the growth and increased the abundance of consumers. Among others in periods of high primary production a great abundance and benthos production was observed (KA-JAK and DUSOGE, unpublished data). A close dependence on food was also noticed when investigating chosen species — such as Leptodora, Chaoborus, Procladius (KAJAK and DUSOGE 1970, HILLBRICHT-ILKOWSKA and KARABIN 1970, KAJAK and RANKE-RYBICKA 1970). In the majority of these situations the dependence of production on the amount of available food is clearly visible. This dependence is expressed either in a decrease of food ration at the simultaneous decrease of the amount of food in habitat, or by a very high indicator of utilization of the food taken for growth. Of course this is not food in general, but the food available and its value. And so e.g. plankton communities chose out of the entire food mass in water only small algae and bacteria, which are only a small part of the total vegetation biomass (GLIWICZ 1969 a). The dominant benthic group — Chironomidae feeds almost exclusively on algae, which are hardly 15% of the sediment mass (KAJAK and WARDA 1968). Benthos consumes algae, which because of the size of their cells cannot be used by plankton.

Great variation of trophic conditions — participation of nannoplankton in production and biomass, its activity etc. has been already mentioned at the beginning. This is valid both in the aspect of time and in various habitats.

The problem of different food utilization by zooplankton communities in different habitats (Table IV) is connected with it. In oligotrophy primary production is directly utilized to a greater extent — in case of eutrophy — to a greater extent in the next production stage, taking the form of bacteria cells, and so the primary production is utilized less effectively. But, it can not be said that the zooplankton production is more effective in oligotrophy than in eutrophy, perhaps it requires great energy expenditures in order to obtain food as its concentration is very small (BLAŻKA 1966). These matters — production efficiency in natural situations — require more intense investigations.

Table IV. Participation of respective components in the food of natural zooplankton species from various types of lakes (acc. to GLIWICZ 1969a)

Lakes	Food components		
	nannoplankton algae	detritus	bacteria
Oligo- and α-mezotrophic	44.0 20—55	18.5 9—30	37.5 25—50
Eu- and β-mezotrophic	12.0 5—24	14.0 7—20	74.0 56—88

It has been mentioned above about the rather great "balancing" of the relations food-consumer, about the fact that the food is utilized to a great extent, that each decrease in the amount of food is reflected in the development of consumers and contrariwise — each increase in the number of consumers — on a decrease of the amount of food in the habitat and worse feeding conditions. So much can be said about simplified situations, when only the feeding conditions are analysed and even when natural food is applied. In experiments with the entire communities of organisms the consequences are greater. This may be illustrated on the example of benthos. Increasing the density of consumers of the first order caused a decrease of the amount of food in the habitat (KAJAK et al. 1968), and as a result of that a decrease of the amount of food in the alimentary canals, decrease of condition, growth rate etc. (KAJAK 1968, KAJAK et al. 1968). Therefore the availability of the consumers of the first order for the predator increased and the predator increased in number (Fig. 5, acc. to KAJAK 1968). On the whole all changes in any one of the elements of habitat or benthos biocenosis cause changes in the number and activity of other biocenotic elements (KAJAK 1968). E.g. the feeding intensity of Chironomidae was greater in mixed slime than when compared with that in slime of an undisturbed structure. Simple, mechanical complication of the habitat structure caused a better utilization of trophic resources and an increase in the abundance of benthos (KAJAK 1968). The productive aspects of these matters are not very well known. There is no doubt that learning about the regularities of functioning of biocenosis is most important in order to understand and organize the production.

Summing up what has been previously said the following investigations starting with species and ending with ecosystems should be carried out in the nearest future:

1) More intense laboratory investigations on energy balances of more important species and in different situations.
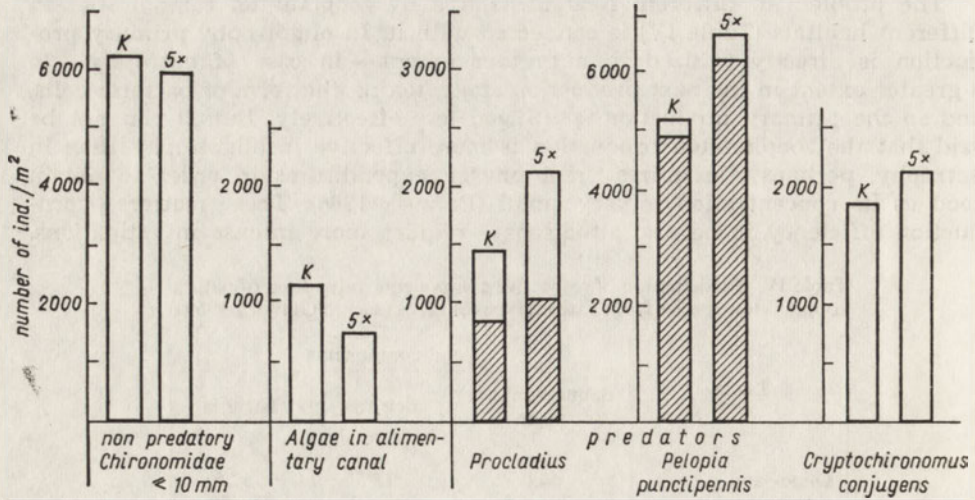
4*

Fig. 5. The effect of artificial increase in number of *Chironomus plumosus* larvae on the number and development of Chironomidae. K — control, 5x — 5 times increase of the number of *Chironomus plumosus*

It is important that these investigations should be carried out in conditions of close confrontation with conditions, in which the given species lives in nature — in the sense of quality and quantity of food, physico-chemical situation etc. Among others essential would be to investigate the significance of the variation of conditions, e.g. thermic, food (quantity and quality of food), light — all these things that exist in nature, but are rarely taken into account in laboratory investigations. Laboratory investigations allow to obtain several results impossible to be achieved in the field, and the data are usually more precise.

2) Investigations on the production mechanisms in natural or close to natural conditions with the entire organisms communities. The research would be carried out in order to determine most precisely the production of neighbouring trophic levels, and so e.g. zooplankton and its food (algal nannoplankton, bacteria, detritus, benthos and the inflowing to it tripton). It is possible and advisable to complicate these matters by taking into consideration higher trophic levels (invertebrate predators and fish) by a simultaneous investigations of plankton itself, its undecomposed remains being the food for benthos and the benthos alone. Also necessary would be a parallel analysis of habitat and also of some transformations of habitat conditions including trophic conditions — either as physico-chemical changes (e.g. transformation of amorphous organic substance into a molecular one) or as the activity of organisms — e.g. faeces production of zooplankton.

Compiling a vast amount of this type of information about the efficiency together with data on the number, species composition domination and other features of investigated communities should allow in future to foresee and determine the function of communities on the grounds of the structural features alone (i.e. domination, composition, number etc.). Only by an analysis of production mechanisms in various situations, and in experimental ones created on purpose one can expect to find out the principles of organizing the

production. Examples have been given of limiting the production by means of food. This took place of course at a simultaneous non-utilization of a considerable mass of primary production by animal consumers because of its inaccessibility. Learning about the factors ccntrolling the occurrence of respective species and communities of producers, and the relations food-consumer is therefore a matter of principle to understand the production regularities.

It would be advisable to cover in these investigations a wide variety of conditions. These may be natural situations and also experimental ones taking place by accident (e.g. feed heating, inflow of sewage waters etc.), and situations created specially for the experiment (e.g. concentration of consumers, various food concentrations, addition of different kinds of food, fertilization etc.).

3) Of course investigations of the entire ecosystems would be still advisable. As these investigations are complex and take a lot of time, it seems that apart from a production estimation of respective links a stress should be put on the extreme links — primary production and production of tripton, and possibly other productions links leaving the water body (catches of fish, reed exploitation etc.).

4) Of course the second item — regularities and mechanisms of production in sections of ecosystems and the third item — analysis of the entire ecosystems, would still require a lot of work in order to improve the reliability of production estimation.

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BIOENERGETIC BUDGETS AND THEIR APPLICATION FOR ESTIMATION OF PRODUCTION EFFICIENCY

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ABSTRACT

Definitions are given, and the basic notions of respective parameters and efficiencies are discussed in instantaneous and cumulative energy budgets, and also their usefulness to characterize respective species and their populations as convertors and energy carriers in trophic chains and between trophic levels in the ecosystem. Special attention is paid to two different methods of calculating population production: 1) sum of biomass increment, 2) sum of elimination, and to their usefulness in calculating population energy budget and efficiencies. Several examples of cumulative energy budgets for individual development are given, and also an example of applying such budgets for field population.

Recently problems of biological productivity have become more popular among biologists. This is mainly due to the activities of the International Biological Programme, which is concerned with investigations on energy flow through living organisms and their communities. Our symposium, which marks the 50th anniversary of the Nencki Institute, also takes the opportunity to present the results of investigations, to a considerable extent inspired by the IBP.

It is useful to recall certain phenomena as they would be useful in further considerations. The computation of energy budgets of single animal species throughout their whole life story, of their field populations, of multi-specific communities, or even of entire ecosystems is, generally speaking, earned out in order to characterize these species or communities as convertors transforming part of the chemical energy contained in food into a similar chemical energy in living bodies, at the cost of dissipation into heat of the rest of this food energy. The investigation of Hiratsuka on the silkworm (1920) was one of the first on the subject of energy transformation of food into body biomass of the consumer. But, we are indebted mainly to Ivlev (1938, 1939 a, b, c, 1945, 1966) for the development of theoretical ideas about energy transformations in the process of biological production. Of course, previously the energy transformations in the processes of growth and development were also the subject of great interest. It is enough to mention that, for some considerable time, a feeding coefficient had been used, which expresses in weight units the

amount of food that has to be eaten by a given animal (pigs, cattle, fish, birds) in order to increase its weight by one identical weight unit. Among the latest synthetical approaches to the bioenergetical trend in ecology we may mention: LINDEMANN 1942, SLOBODKIN 1959, 1962, KLEIBER 1961, MACFADYEN 1964; PHILLIPSON 1966. The development of bioenergetics in hydrobiology owes a great deal to WINBERG (1956, 1962, 1964, 1965, 1966, 1967, 1968). It should be also added, that, although many of the important discoveries and generalizations were revealed in hydrobiological investigations, the recent studies of terrestrial organisms and ecosystems have contributed significantly towards the further development of this field of sciences, e.g. PETRUSEWICZ (ed.) 1967 c. Energetically, there are no essential differences between the phenomena of energy flow through aquatic and terrestial ecosystems, at least with respect to energy balances and indicators of energy conversion.

Energy budgets

An energy budget is an equation expressed in units comparable from the energy point of view (it is the best in calories), in relation to some period of time. In this equation the amount of energy flowing in as food to the individual or community is expressed as a sum of elements presenting the further fate of this energy. Using the symbols based on PETRUSEWICZ 1967 b, RICKER 1968, KLEKOWSKI and DUNCAN in print a, the balance equations will be as following

$$C = P+R+U+F = D+F \tag{1}$$

$$D = P+R+U \tag{2}$$

$$A = P+R \tag{3}$$

where: C — consumption, food intake; D — digestion, part of the food that is digested and absorbed; P — production, may consist of P_g — the growth of the body, and P_r — production of the organic material, which is passed out into the environment during the life of animal (reproductive products, milk, exuvia, moulted hair, feathers, reptile skin, spiders' webs, silk, beeswax, venoms, odorants etc.); R — respiration, cost of maintenance; F — unabsorbed part of consumption; U — urinary and other "waste" part of digestion; FU — when difficult to separate U from F, and treated together; A — assimilation, sum of production and respiration, food absorbed less the excreta.

As it has been already said all parameters of energy budget should be related to a defined period of time[1], i.e. to determine the rate of flow and accumulation of energy in an organism or community of animals. It can be easily seen, that the application of true, i.e. differential rate (dx/dt), when dt tends to zero, is incorrect, as the processes of absorbing and transforming the food energy by animals are either discontinuous, or their rate vary, or are not synchronized. Therefore the energy budget is usually presented as average rates for some arbitrary chosen time unit $(\Delta x/\Delta t)$, which is usually 24 hr. This reference time unit Δt should not be mixed with the choice of adequate period

[1] The following denotations of time will be applied: ... t_{n-1}, t_n ... — general unspecified time (hours, days, etc.); τ_0 ... τ_{n-1}, τ_n ... — animal age (days or other units); T_0 ... T_{n-1}, T_n ... — time of population (cohorts, generation, group of one age or other distinguished group) story.
N.B. If in further considerations various denotations for time are applied simultaneously, their units are the same, e.g. days.

of time for the experimental measurement of respective budget parameters. The duration time of such measurement will depend on the period of species feeding, defecation or respiration cycles and on the feeding biology of the species being investigated (for a discussion of this problem, see DUNCAN and KLEKOWSKI in print, KLEKOWSKI and DUNCAN, in print b). Such an energy budget for a specified moment in the life of an individual (τ_n) or population T_n may be termed "an instantaneous energy budget".

The basic energy parameters used in instantaneous budgets (C_i, P_i, R_i) can be combined in the form of non-dimensional ratios or percentages, which are called coefficients of efficiency or simply efficiencies. They were introduced into bioenergetics by IVLEV (1939 a, b, c), and later developed theoretically by WINBERG (1956, 1962, 1965, 1967, 1968). KOZLOVSKY (1968) has given a comprehensive and useful review of various efficiencies applied in ecological investigations (compare also discussion of this problem in KLEKOWSKI and DUNCAN in print a, DUNCAN and KLEKOWSKI in print). Thus the efficiencies are:

$$U_i^{-1} = \frac{P_i + R_i}{C_i} = \frac{A_i}{C_i} \qquad \text{assimilation efficiency;} \qquad (4)$$

$$K_{1i} = \frac{P_i}{C_i} \qquad \text{efficiency of utilization of consumed energy for growth (after WINBERG);} \qquad (5)$$

$$K_{2i} = \frac{P_i}{P_i + R_i} = \frac{P_i}{A_i} \qquad \text{efficiency of utilization of assimilated energy for growth (after WINBERG).} \qquad (6)$$

As for the above non-dimensional ratios, parameters of instantaneous budgets were used, these efficiencies should have also similar denomination, e.g. instantaneous coefficient of assimilation efficiency and so on.

Computation of budgets for successive days in the life of an individual (τ_1, τ_2, τ_3 ... τ_n) illustrates well the changes in the intensity of feeding, respiration, growing etc.

When these budget parameters are estimated for animals cultivated in various conditions of the environment, we can trace the effect of these conditions on developmental changes of mentioned parameters (e.g. different food concentrations; KLEKOWSKI and SHUSHKINA 1966).

Figure 1 presents the changes of daily rates of C, P, R and instantaneous efficiencies U_i^{-1}, K_{1i}, K_{2i} of *Macrocyclops albidus* at food concentration 1 g wet wt/m³. But Figure 2 illustrates the changes of consumption and respiration (R_i) of successive developmental stages depending on the food concentration. Such instantaneous energy budget and efficiencies of energy conversion characterize well the physiological properties of a given species at an individual level, and also the changes in these properties in relation to developmental stage, physiological state and environmental conditions. These parameters of individual instantaneous energy budget are measured either in conditions similar to those in which the natural population of this species lives or some "correction coefficients" (e.g. normal Krogh curve for the dependence of R_i on temperature, or some recalculations for different feeding conditions) may be applied, then the energy budget for such population can be calculated. Therefore a simple multiplication should be made of the number of individuals (N), given sex, stage, age or size by the value C_i, P_i etc., which is characteri-
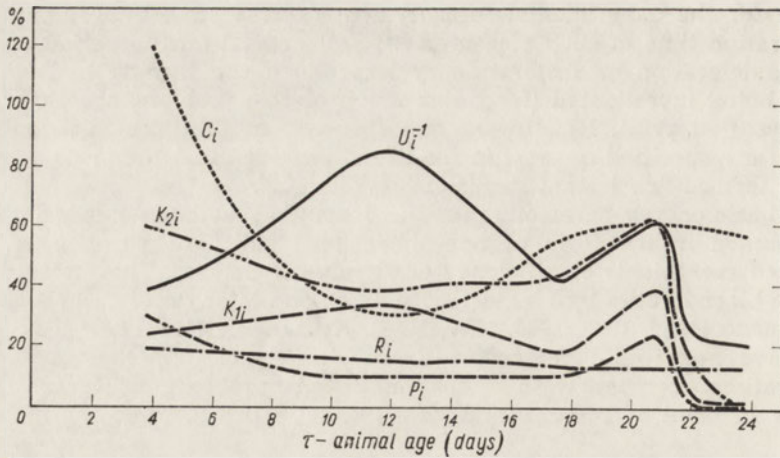
Fig. 1. Changes of daily rates of consumption, respiration and production (as %
of body's calorific value) and instantaneous efficiencies U_i^{-1}, K_{1i}, K_{2i} in *Macrocyclops albidus*; in food *concentration* 1g wet wt./m³; the period before reproduction
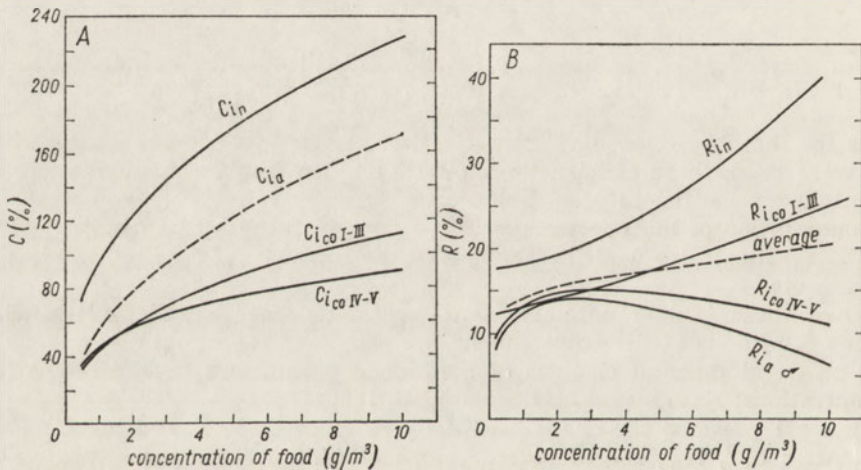(after KLEKOWSKI and SHUSHKINA 1966)

Fig. 2. The relationship of instantaneous parameters of energy budget of different
developmental stages of *Macrocyclops albidus* to food concentration. A — Daily
rates of consumption (C_i) as % of body's calorific values (unpubl. materials); B —
Daily rates of respiration (R_i), as % of body's calorific values (after SHUSHKINA and
KLEKOWSKI 1968); n — nauplii; co I–III — copepodits I–III; co IV–V — copepo-
dits IV–V; a — adults

stic for this sex, stage, etc. The results obtained should be summed up. And
therefore e.g.

$$C_{i\,pop.} = C_{ia} \cdot N_{ia} + C_{ib} \cdot N_{ib} \ldots,$$

where: a, b belong to the above mentioned groups of individuals in the popu-
lation (of the given sex, age, size etc.). Thus, generally speaking, proceeded

MANN in his work (1964) on production and bioenergetical characteristics of fish population in Thames (in further paper (1965) MANN used growth and death rates).

Such an energy budget gives first of all information about the intensity with which the given population acts on its environment, i.e. how much food is eaten, the amount degraded to FU and the amount of oxygen used for transforming the part of this food into heat. The remaining and perhaps the most important parameter, P, requires a detailed analysis, and is dealt with later on.

Attention should be paid to the fact that instantaneous efficiencies can be calculated only in situations when in the energy budget equation (1) C and $P > 0$, i.e. when the given individual is feeding and producing. However, among many groups of animals during their normal individual development there are stages or periods, during which the animals do not consume food, or the consumption is too small to satisfy the needs of respiration. In both these situations the production is "negative" (in the sense used by PETRUSE-WICZ 1967 a), i.e. the animal loses part of the energy previously accumulated in the body. Such a situation is typical for holometabolic insects, e.g. during the development of the terrestrial beetle *Tribolium castaneum* (see later, p. 69) "negative" production takes place during the development of the egg and pupa, when the animal does not consume food at all, or in very young larvae or very young adults — when underfeeding occurs (KLEKOWSKI et al. 1967). Similarly, during the pre-imaginal development of stored product pest *Rhisoglyphus echinopus* (Acarina) (see p. 72) there occur three periods of feeding and active growth alternating with periods of "physiological starvation" and loss in both body weight and calorific value (KLEKOWSKI and STĘ-PIEŃ in litt.). Of course instantaneous efficiencies cannot be calculated for such periods of "negative" production.

The "cumulative energy budget" proposed by KLEKOWSKI et al. (1967), does not have such limitations. In order to calculate the parameters of such budget all the parameters in equation (1) are cumulated from the beginning of the life cycle (time τ_0) to the successive moments (successive days) of its life ($\tau_1, \tau_2 \ldots \tau_n$). The elements of a cumulative budget may be defined as follows:

$$C_c = \int_{\tau_0}^{\tau_n} C_i(\tau)dt \approx \sum_{\tau_0}^{\tau_n} C_i \quad \text{food consumption cumulated from } \tau_0 \text{ to } \tau_n; \quad (7)$$

$$R_c = \int_{\tau_0}^{\tau_n} R_i(\tau)dt \approx \sum_{\tau_0}^{\tau_n} R_i \quad \text{respiration cumulated from } \tau_0 \text{ to } \tau_n; \quad (8)$$

$$FU_c = \int_{\tau_0}^{\tau_n} FU_i(\tau)dt \approx \sum_{\tau_0}^{\tau_n} FU_i \quad \text{un-assimilated food cumulated from } \tau_0 \text{ to } \tau_n; \quad (9)$$

$$P_c = \int_{\tau_0}^{\tau_n} P_i(\tau)dt \approx \sum_{\tau_0}^{\tau_n} P_i = B_{g\tau_n} + \sum_{\tau_0}^{\tau_n} P_{r_i} = B_{g_i\tau_n} + B_{r\tau_n} \quad \text{production} \quad (10)$$

of body growth, reproductive and other products cumulated from τ_0 to τ_n, where: $B_{g\tau_n}$ — biomass in energy units of body at τ_n, $B_{r\tau_n}$ — sum of P_r from τ_0 to τ_n.

The above equations are given in integral terms, whereas in practice the calculation of cumulative parameters is obtained from summation of the daily consumption (respectively: respiration etc.) for each day in the life of the individual or an average individual.

Combining the cumulated budget parameters C_c, P_c, R_c in the form of non-dimensional ratios, cumulative coefficients of efficiency may be obtained as follows:

$$U_c^{-1} = \frac{P_c + R_c}{C_c} = \frac{B_g + B_r + R_c}{C_c} = \frac{A_c}{C_c}$$

cumulative assimilation efficiency; (11)

$$K_{1c} = \frac{P_c}{C_c} = \frac{B_g + B_r}{C_c}$$

cumulative efficiency of utilization of consumed energy for growth; (12)

$$K_{2c} = \frac{P_c}{P_c + R_c} = \frac{B_g + B_r}{B_g + B_r + R_c} = \frac{P_c}{A_c}$$

cumulative efficiency of utilization of assimilated energy for growth. (13)

This method of regarding and expressing energy budgets and efficiencies in cumulative form provides two kinds of information about the species being studied.

Firstly, it is possible to asses for each moment of the life of an individual or an average individual the amount of energy that must be consumed in the food, dissipated as heat, and degraded as *FU*, in order to allow the animal to attain a certain size or stage of development. And in such budget all the periods of "negative growth" are taken into consideration. The cumulative efficiencies computed from these cumulative parameters characterize the species as an "energy carrier" between its food and the following trophic level. It is obvious, that these efficiencies (K_{1c}, K_{2c}) of energy transfer depend fundamentally on the moment, in which the body or products of the animal under study will become the food of the successive link in the food chain. The further examples of cumulative budgets and efficiencies will illustrate this statement.

Secondly, knowing the cumulative budget of the species, in conditions approximating to those in which its field population lives, such a budget of an average individual (taking into consideration the differences between ♀ and ♂ — if useful) can be used to compute the bioenergetical characteristics of such population.

Before presenting examples of laboratory cumulative budgets and an attempting to apply the method of cumulative budgets to a natural population[2] it is worth considering which out of the several ways of understanding the notion "biological production" is appropriate for the needs of ecological bioenergetics. Although this notion is differently understood (review by PETRUSEWICZ 1967 a, KACZMAREK 1967) the ways of calculating the production may be reduced to two:

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[2] The expression "population" is in our considerations equivalent to notions: cohort, generation, one-age group etc. In species with several generations per year, which are distinguishable, it is still possible to calculate the production and other parameters of energy budget of whole population by working and calculating in generation periods separately and then adding together to obtain integrated results.

1) "Sum of increments". Population production for the period $t_{n-1}-t_n$ is a sum of energy in the increments, during the time $t_{n-1}-t_n$, of all individuals belonging to this population including their sexual products, young ones and other products. This is how the production of population is understood by the majority of ecologists (e.g. PHILLIPSON 1967, PETRUSEWICZ 1967 a, WINBERG 1962, 1967, 1968, EVANS 1967, MACFADYEN 1967).

The mathematical formula (e.g. acc. to PHILLIPSON 1967) is as following:

$$P_{t_{n-1}-t_n} = \left(N_{t_n} \cdot \frac{\Delta B}{\Delta t}\right) + \left(\frac{\Delta N}{\Delta t} \cdot \frac{1}{2} \cdot \frac{\Delta B}{\Delta t}\right) \tag{14}$$

where:

$P_{t_{n-1}-t_n}$ — population production for the period $t_{n-1}-t_n = \Delta t$ (e.g. between two measurements of number and standing crop);

N_{t_n} — number of survivors at t_n;

$\dfrac{\Delta B}{\Delta t}$ — increase in individual biomass from body growth, reproductive products etc. during period Δt;

$\dfrac{\Delta N}{\Delta t}$ — number of animals, which died during the period Δt.

Factor $\dfrac{1}{2}$ — it is assumed that growth and mortality rates are constant during the period Δt.

Computation of the total population production for a period of time T_0-T_n, covering more than one period of Δt, is in this method a summation of population increments for this entire period:

$$\int_{T_0}^{T_n} P(T)dt \approx \sum_{T_0}^{T_n} P = \sum_{T_0}^{T_n} \cdot \left[\left(N_{t_n} \cdot \frac{\Delta B}{\Delta t}\right) + \left(\frac{\Delta N}{\Delta t} \cdot \frac{1}{2} \cdot \frac{\Delta B}{\Delta t}\right)\right] \tag{15}$$

2) "Sum of elimination". Population production for the period $T_{n-1}-T_n$ is a sum of energy, in the form of individuals that died within that period, their dead young ones, dead eggs, and non-living organic products, which has been eliminated thus transmitted to other trophic levels (or even within the same trophic level, e.g. via lactation and cannibalism). Such an interpretation of production has been much more rarely taken in ecology: CCOPER (1965) in his investigations on amphipod *Hyallela azteca* understood production as the number (and biomass) of animals that are removed from the population as "yield"; BOCOCK et al. (1967) defined the production similarly as a biomass of dead animals, eliminated eggs and exuviae. However, PETRUSEWICZ (1967 a, b) understood the population production as a "sum of increments", but says that the production removed by predators and decomposed or "emigrated" (elimination) is different from the biomass increment. Therefore:

$$P_{t_{n-1}-t_n} = \left(\frac{\Delta N}{\Delta t} \cdot \frac{\overline{B}_{gt_{n-1}} + \overline{B}_{gt_n}}{2}\right) + (\Delta B_r) \tag{16}$$

where:

$\overline{B}_{gt_{n-1}}$ — average individual biomass (in energy units) of the population, in the moment t_{n-1};

$\bar{B}_{gt_n}$ — average individual biomass (in energy units) of the population, in the moment t_n;

ΔBr — biomass (in energy units) of reproductive products dead in the period Δt and of other non-living products "lost" by all members of the population in the period of time Δt.

Therefore the total population production for the period $T_0 - T_n$ (comp. 15) would be:

$$\int_{T_0}^{T_n} P(T)dt \approx \sum_{T_0}^{T_n} P = \sum_{T_0}^{T_n} \cdot \left[\left(\frac{\Delta N}{\Delta t} \cdot \frac{\bar{B}_{gt_{n-1}} + \bar{B}_{gt_n}}{2} \right) + (\Delta B_r) \right] \qquad (17)$$

In order to demonstrate the differences and similarities of the results of calculating production from "increments" or from "eliminations", Figure 3A presents the changes in the number (N) of hypothetical population and the changes of biomass of an average individual and the eggs it laid. The parameters of this "invented" population are as following: annually 100 eggs· ·0.2 cal = 20 cal/m² are "brought forward" from the preceeding year (or cycle). During the year (cycle) there are 5 periods: in the I period the individual grows to 4 cal, in the II period — from 4 to 6 cal, in the III period the individual loses 3 cal out of 6, in the IV period remains without any changes during the egg production. All the individuals die during the I–IV period with a constant mortality rate. During the IV period each individual lays on the average 10 eggs, and thus in the end of that period N eggs/m² = 125. In the V period a reduction takes place of 25 eggs/m² and again 100 eggs/m² remain.

Figure 3B presents the cumulated production of this population calculated according to formulae (15) and (17). As it can be seen the production cumulated for the entire year is exactly the same (370 cal/m²) independent of which formula has been applied. But for shorter periods, the formulae provide different information; one shows when the bulk of production takes place, the other gives information on when and to what measure this production becomes available to other trophic levels, predators or decomposers. Thus it is without any significance for other trophic levels that our population had produced by the end of the II period as much as 457.5 cal/m² (curve 1 on Fig. 3B), because already during the following III period, this cumulated production had decreased to 345 cal/m² as a result of loss of biomass due to the respiratory needs of the non-feeding stages. Examples of cumulative budgets given later in the text will demonstrate that such metabolic loss of body weight during periods of "physiological starvation" are not exceptional.

Now we can try to estimate the usefulness of the two methods production calculation for energy budgets of populations.

A. In order to prepare such budget by calculating the production with the method of the "sum of increments", it is necessary to compute all the remaining parameters of the budget (C, R, FU) using formulas analogous to (14). For example, formula (14) for respiration would be:

$$R_{t_{n-1}-t_n} = \left(N_{t_n} \cdot \frac{\Delta R}{\Delta t} \right) + \left(\frac{\Delta N}{\Delta t} \cdot \frac{1}{2} \cdot \frac{\Delta R}{\Delta t} \right) \qquad (18)$$

where: ΔR — average respiration of survivors during the period Δt.

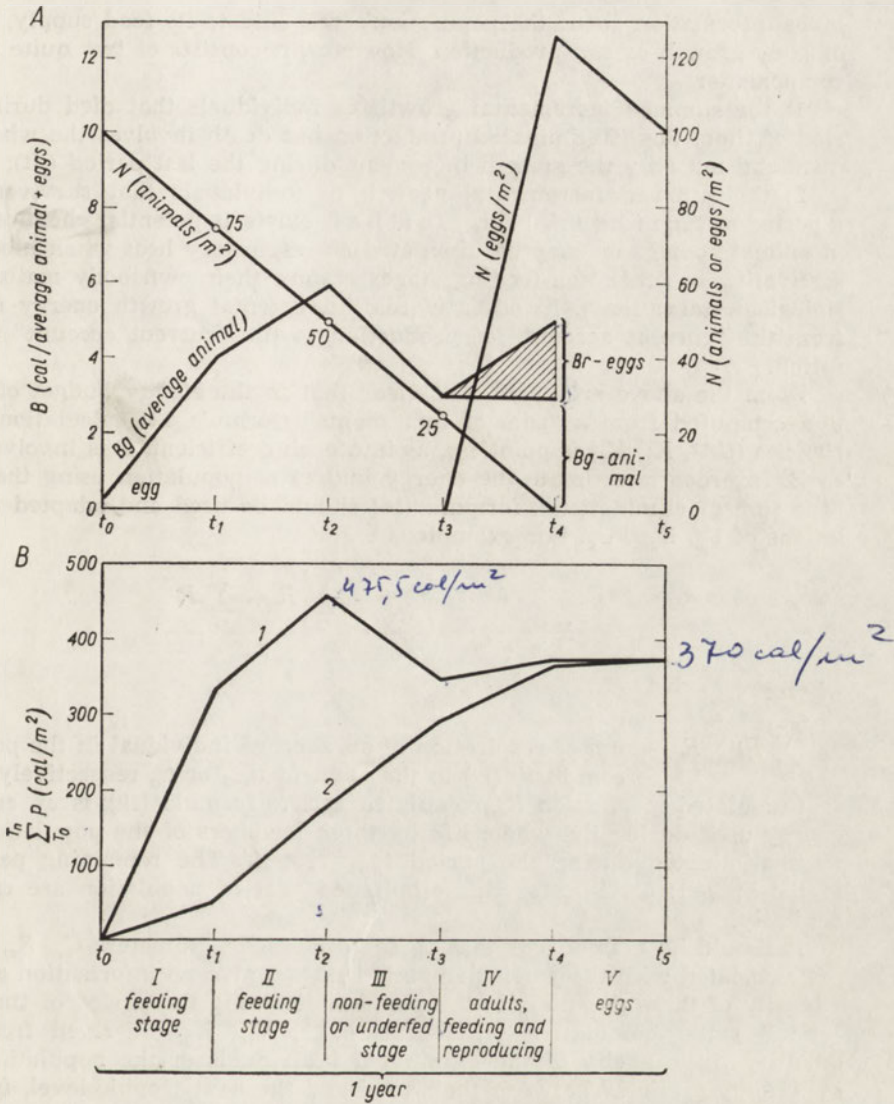R calculated from formula (18) is the amount of energy used for respiration

Fig. 3. Hipothetical population having one short reproduction period. A — Abundance of animals and progeny (eggs); change in the individual's biomass and of the sum of eggs it produces. B — Cumulated production of population calculated by two methods: 1 — "sum of biomass increments" (formula 15), 2 — "sum of elimination" (formula 17)

by a population during the period $t_{n-1} - t_n$. Thus the calculated parameters (C, R, FU) characterize well the tropho-dynamic (in the sense used by LINDEMANN 1942) relationship of the given population with its food supply in a given period of time; they give information about the food energy intake (C), about the energy returned to the ecosystem (FU) and about the energy dissipated as heat (R). The production (P), as calculated from formula (14),

gives information about the population's response to its food supply, in terms of body growth or egg production. However, it consists of two quite different components:

1) the summed incremental growth of individuals that died during a period of time; this is eliminated production but death involves the whole organism and not only the growth increment during the last period (Δt);

2) the summed incremental growth of individuals that survived during a period of time (Δt); this energy e i t h e r exists as potential chemical energy in animal bodies o r may be dissipated as respiratory heat when hibernating, aestivating or other non-feeding stages respire their own body matter ("physiological starvation"). In other words, incremental growth energy is passed from the "current account" of production to the "current account" of respiration.

From the above argument it is clear that in the energy budget of population computed from a "sum of increments" (formula 14) calculation of efficiencies (U^{-1}, K_1, K_2) is pointless, as into each coefficient, P is involved.

B. In order to estimate the energy budget of population using the method "the sum of elimination", formula (16) should be used and adapted to calculations of C_c, R_c, FU_c. For example:

$$R_{c\,t_{n-1}-t_n} = \frac{\Delta N}{\Delta t} \cdot \frac{\sum\limits_{\tau_0}^{t_{n-1}} R + \sum\limits_{\tau_0}^{t_n} R}{2} \tag{19}$$

where:

$\sum\limits_{\tau_0}^{t_{n-1}} R;\ \sum\limits_{\tau_0}^{t_n} R$ — sum of respiration of an average individual in the population from birth (τ_0) to the moment t_{n-1} or t_n, respectively.

Cumulated respiration R_c, calculated acc. to formula (19), is an amount of energy used during the whole life by those members of the population which were eliminated during the period $t_{n-1}-t_n = \Delta t$. The remaining parameters of the budget: C_c, FU_c for this eliminated part of population are calculated similarly.

It should be pointed out that these cumulated parameters C_c, R_c, FU_c are not associated with the particular period Δt and give no information about the intensity of these processes in the population during the period of time $t_{n-1}-t_n$. But the cumulative efficiencies (U_c^{-1}, K_{1c}, K_{2c})[3] derived from them, quantify the capacity of the eliminated individuals of the population to act as "energy carriers" between their food and the next trophic level, for which they themselves serve as food. If the population belongs to the trophic level n then its cumulative efficiencies for eliminated production are:

$$U_c^{-1} = \frac{A_c}{C_c} = \frac{\text{assimilation at } n}{\text{consumption at } n, \text{ from } n-1} \tag{20}$$

[3] Some difficulties arise, when taking into consideration the "costs of production" of ΔBr (see formula 16) in formulae of such type as (19). This cost is not taken into account in formula (19), because the individuals, which produce eggs and other products may live considerably longer after the time t_n. It seems that this difficulty can be overcome, at least for the reproductive products, applying the "inter-generation cumulative budget" (see further on the example of energy budget of *Rhisoglyphus echinopus* p. 72).

$$K_{1c} = \frac{P_c}{C_c} = \frac{\text{energy passed to } n+1}{\text{consumption at } n, \text{ from } n-1} \qquad (21)$$

$$K_{2c} = \frac{P_c}{A_c} = \frac{\text{energy passed to } n+1}{\text{assimilation at } n} \qquad (22)$$

Examples of laboratory cumulative energy budgets

As it has been said previously, full cumulative budget requires the possibility of reading all cumulated parameters of budget and efficiencies for each
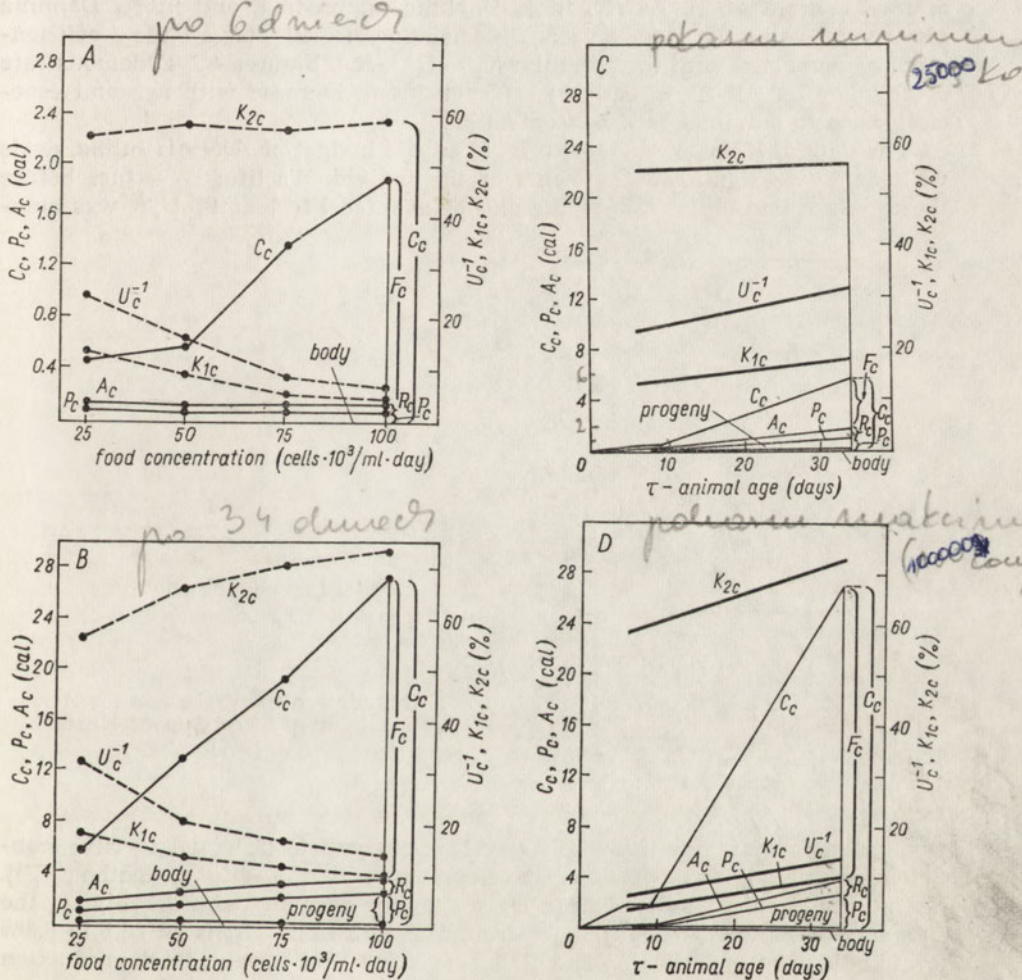

Fig. 4. Energy budget for *Daphnia pulex* (plotted, after some recalculation, after data of RICHMAN 1958). A — In different food concentrations; after 6 days growth: 2–4 days before reproduction; B — In different food concentrations; after 34 days growth: 8–10 days of body growth and 24–26 days of simultaneous body growth and production of youngs; C — Cumulative budget for animals growing in minimal food concentration applied (25,000 Chlorella cells/ml·day); D — Cumulative budget for animals growing in maximal food concentration applied (100,000 Chlorella cells/ml·day)

moment of life. However, data from some papers, can be cumulated in order to produce cumulative budgets. Figure 4 presents the results of the classical paper of RICHMAN (1958) on the energy budget of *Daphnia pulex* in 4 food concentrations (Chlorella). Figure 4A, B is arranged acc. to food concentrations, and 4C, D acc. to the animal's age (τ) — for minimal and maximal food concentrations used by the author. Fig. 4A, B show that the food concentrations applied by RICHMAN were sufficiently small to be found within the range, where food ration depends directly proportionally on the food concentration (SUSHCHENYA 1963). Assimilation (U_c^{-1}) decreases together with an increase of food concentration. As K_{2c} in τ_6 Daphnia is constant, and in τ_{34} Daphnia also changes slightly, the curve K_{1c} is analogous to U_c^{-1} (as all the 3 efficiencies are connected with the formula: $K_1 = U^{-1} \cdot K_2$). Figures 4C, D demonstrate a tendency for all the cumulative efficiencies to increase with age and especially also to maximal food concentration.

The data of KHMELEVA (1967) (Fig. 5) on the budget of *Artemia salina*, deals with only two significant moments of the individual's life: τ_{32} — just before the eggs are laid and τ_{132} — to the end of average life length. U_c^{-1} was assu-
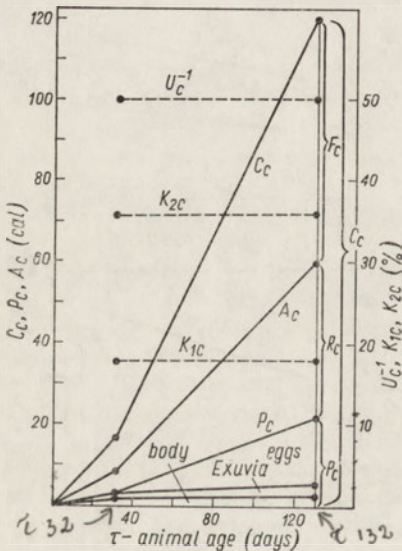

Fig. 5. Cumulative energy budget for *Artemia salina* (plotted after data of KHMELEVA 1967)

med to be constant for the whole development and to be equal to 50% (confirmed for the initial period of development with the help of method C^{14}). K_{1c} and K_{2c}, calculated only for body growth, decrease considerably as the animals become older; K_{1c} changes from 12.6 to 2.3 and K_{2c} from 28.1 to 6.6% in animals aged τ_{32} and τ_{132}. But it is surprising that for the total production (P_c) the efficiencies are the same for both discussed moments of life.

The following filtrator is *Simocephalus vetulus* (KLEKOWSKI and IVANOVA, in litt.). Food — Chlorella; temp. 22°C. Measured parameters — C, R, P_g, with an approximative evaluation of P_r (Fig. 6). All parameters and efficiencies were calculated for subsequent days of life. Body growth takes place during the first eight days and practically stops during the period of reproduction. U_i^{-1} changes greatly during the life of an individual, and that is why U_c^{-1}
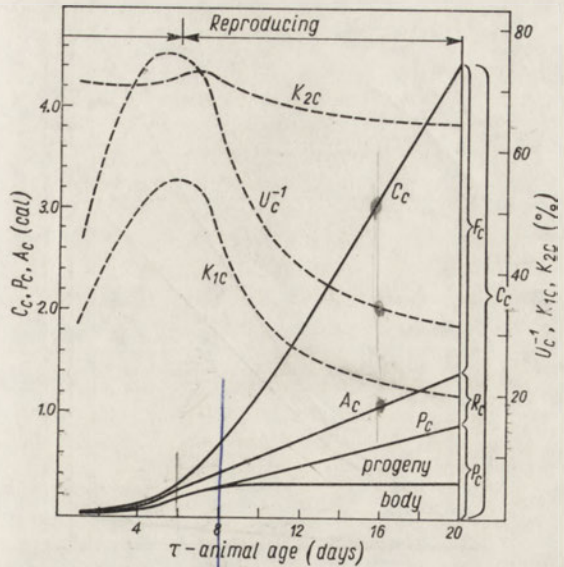
Fig. 6. Cumulative energy budget for whole individual life cycle of *Simocephalus vetulus* (KLEKOWSKI and IVANOVA in litt.)

is also greatly variable — it increases quickly during the period of exponential growth to a maximal value of 75% just before the reproduction begins. Regular decrease in cumulated assimilation during the reproductive period to ca 30% (contrariwise to RICHMAN's Daphnia) is connected with a considerable decrease of instantaneous assimilation efficiency. Perhaps this was caused by the need for specific "building material" (e.g. essential amino acids or lipids) during the production of eggs and embryos. K_{2c} was very high (65–70%) and practically almost constant, the higher values occurring during the exponential body growth. In such a situation K_{1c} will reflect only the changes in assimilation.

Table I presents the budget parameters and efficiencies for the typical development moments of an average animal, *Simocephalus vetulus*. Thus, young Simocephalus utilizes its food especially well during the period of body growth, but not when it is old and during the period when young are produced. Since in most natural populations elimination by predators affects mainly the pre-reproductive and early reproductive stages, it can be assumed, that most of energy carried by *S. vetulus* from filtrators to predators have good coefficients of efficiency.

Figure 7 is a budget for the deposit-feeder, *Asellus aquaticus* (PRUS, unpublished data). Food — decaying alder leaves; temp. 21–23°C. Measured C —

Table I. *Simocephalus vetulus* (after KLEKOWSKI and IVANOVA in litt.).

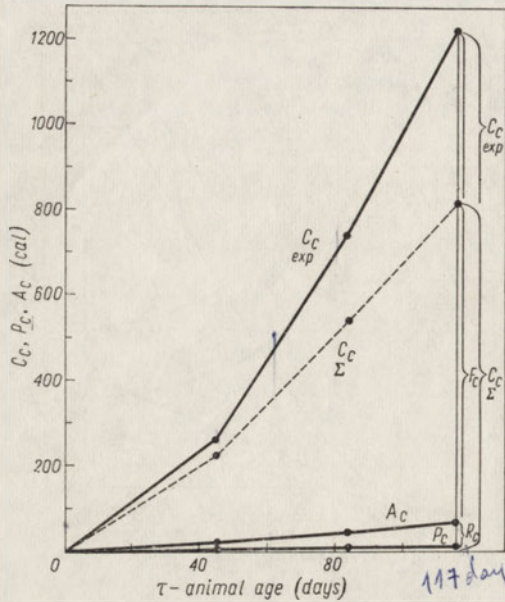| Animal age	τ_n	$\sum_{\tau_0}^{\tau_n}$ (cal $\cdot 10^{-3}$)					%		
		C_c	P_c	R_c	A_c	FU_c	U_c^{-1}	K_{1c}	K_{2c}
Pre-birth ♀♀	7	478	253	93	346.1	131.9	72.4	52.9	73.1
Reproducing ♀♀	20	4482	919	501	1420	3062	31.7	20.5	64.7

Fig. 7. Cumulative energy budget for growing *Asellus aquaticus* (after Prus unpublished)

independently, using two methods: direct gravimetrical, or from the sum $C = P + R + F$, where each of the last three parameters were measured. Figure 7 presents the preliminary results of a cumulative budget. It turned out later that the two measurements of C, however they differed one from another, both were much overestimated due to an inadequate method of wet weights, and therefore were rejected. Only P and C values was back-calculated by assuming the assimilation efficiency of 30.28%, ascertained in further studies (Prus in litt. a). Table II presents data for an average individual of 22 mg wet weight, reached after 117 days of experiment.

Table II. *Asellus aquaticus* (After Prus in litt. b)

Animal age	$\sum_{t_0}^{t_{117}}$ (cal)					%		
	C_c	P_c	R_c	A_c	F_c	U_c^{-1}	K_{1c}	K_{2c}
Growing 117 days from 1.58 mg to 22 mg wet weight +pre-experimental period	253.4	14.2	62.6	76.8	176.6	30.28	5.5	18.2

All the efficiencies are small in *Asellus aquaticus*. Rather low assimilation, is accompanied by an equally small utilization of assimilated energy for growth (less than 20%). K_{1c}, less than 6%, is especially low, considerating that the animals were at the age, when the growth was relatively intense and that food in excess supply.

Worth mentioning are the results of Fischer (1970) on the energy budget of a phytophagous fish *Ctenopharyngodon idella*. Table III presents the instantaneous daily energy budget of fish, fed with Lactuca (for an average animal).

Table III. *Ctenopharyngodon idella* (after FISCHER 1970)

Animal size	(cal)					%		
	C_i	P_i	R_i	A_i	FU_i	U_i^{-1}	K_{1i}	K_{2i}
Body wet weight 20—70 g (mean 30 g)	4.435	0.84	0.539	0.623	3.812	14.0	1.9	14.0

As it can be seen, the order of the values of the coefficients of efficiencies is very similar to those of *Asellus aquaticus*.

Terrestrial holometabolic insect, stored product deposit feeder — *Tribolium castaneum* (KLEKOWSKI et al. 1967). Food — flour with an addition of yeast; temp. 29°C. Measured P_g, P_r, R. As it can be seen in Fig. 8A, periods of under-
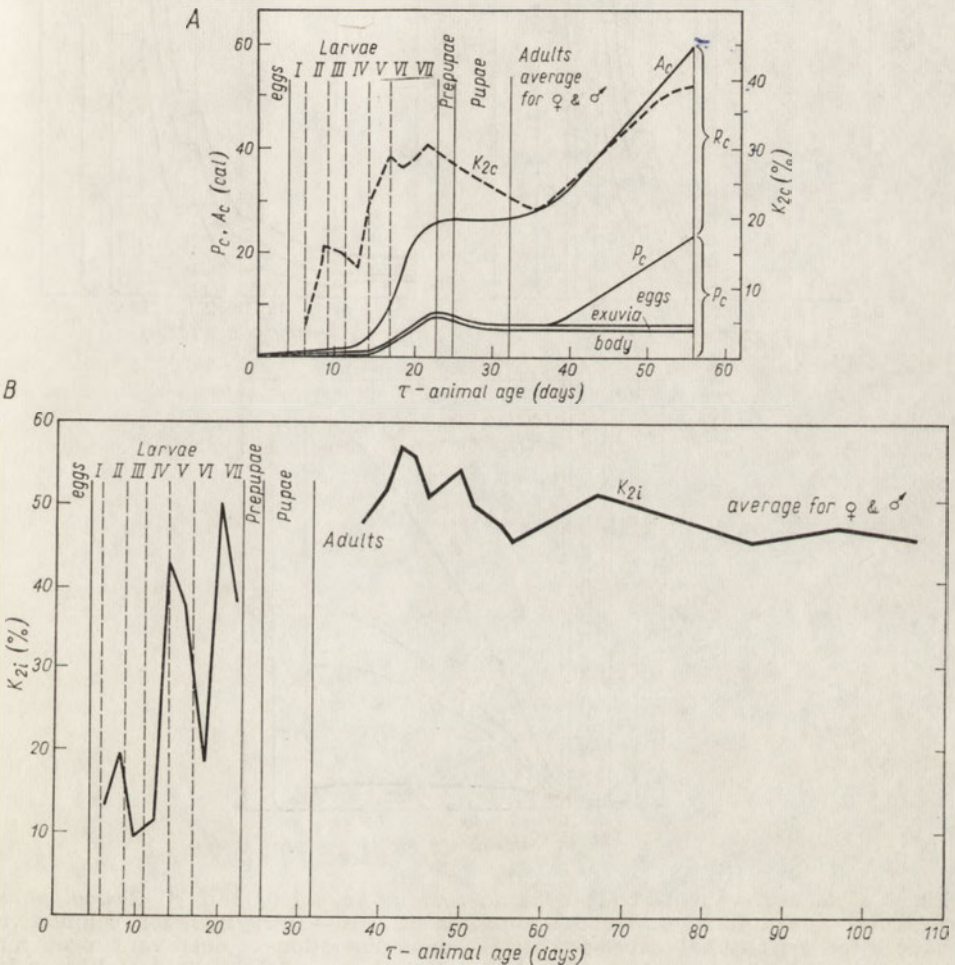
Fig. 8. Cumulative energy budget for an average animal (♀ and ♂) *Tribolium castaneum* (after KLEKOWSKI et al. 1967). A — General picture of cumulative energy budget; B — Changes of instantaneous efficiency K_2
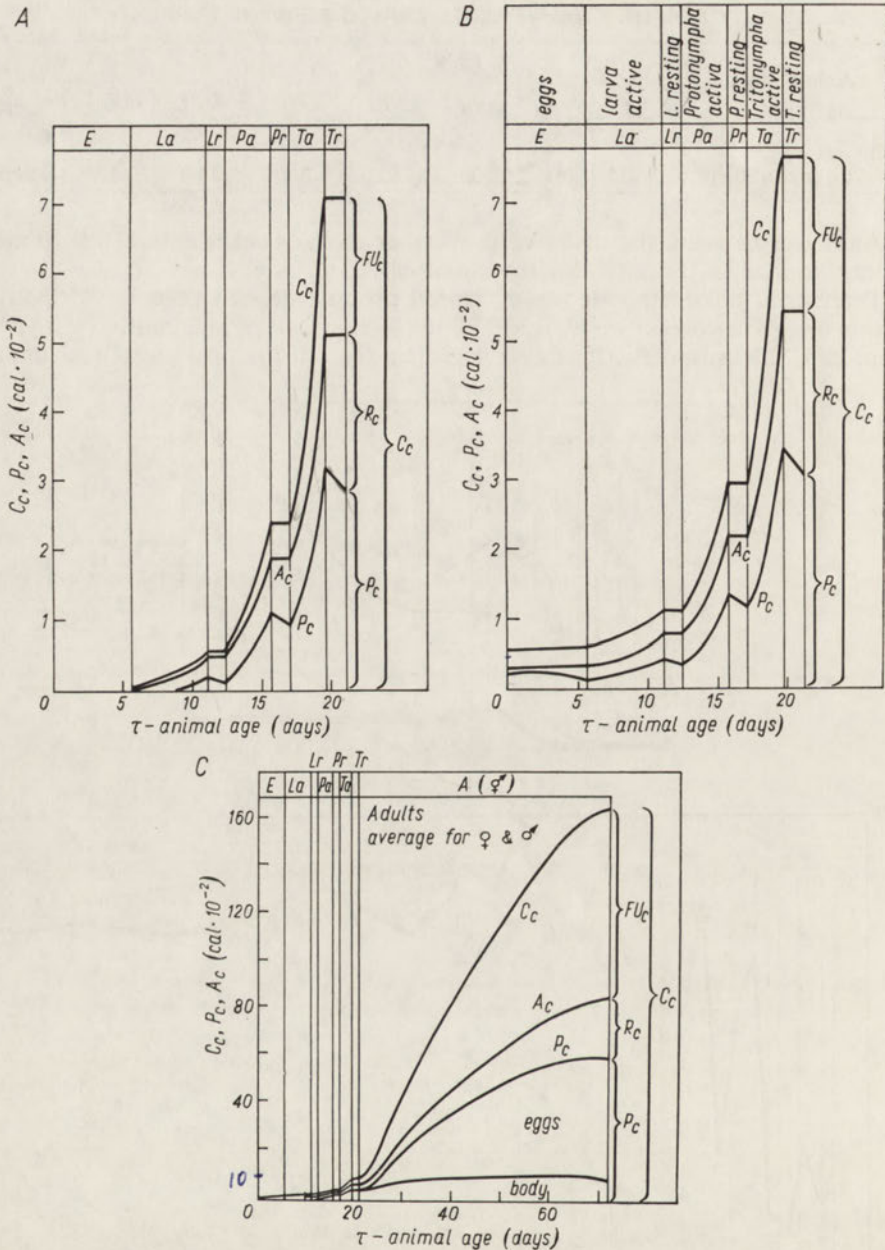
Fig. 9. Cumulative energy budget for an average animal (♀ and ♂) *Rhisoglyphus echinopus* (after KLEKOWSKI and STĘPIEŃ in litt.). A — Intrageneration cumulative budget for preimaginal development; B — Intergeneration cumulative budget for preimaginal development; C — Cumulative budget for whole individual life cycle (on this scale differences between intra- and intergeneration budget are negligible). D — Changes of assimilation efficiency. U_i^{-1} — instantaneous coefficient, U_c^{-1} intra — cumulative coefficient calculated from intrageneration cumulative energy
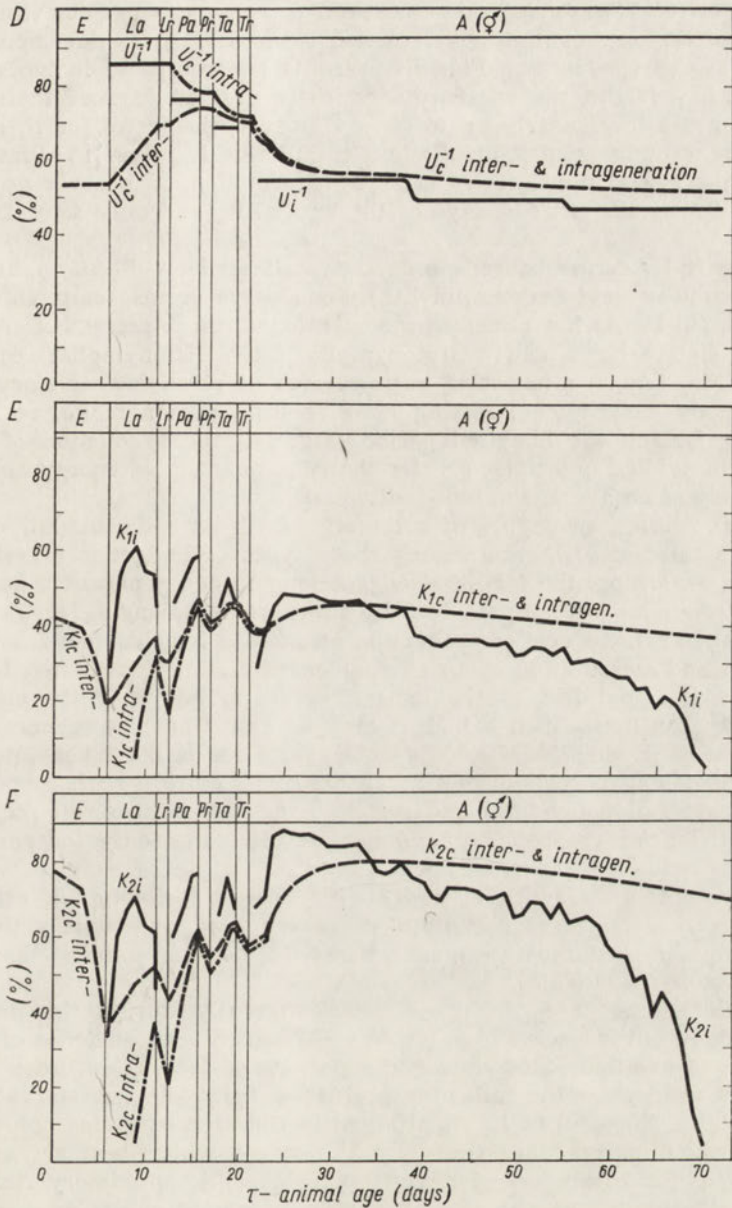
budget, U_c^{-1} inter — cumulative coefficient calculated from intergeneration cumulative energy budget. E — Changes of efficiency of utilization for growth of consumed energy. K_{1i} — instantaneous coefficient, K_{2c} intra — cumulative coefficient calculated from intrageneration cumulative energy budget, K_{2c} inter — cumulative coefficient calculated from intergeneration cumulative energy budget; F — Changes of efficiency of utilization for growth of assimilated energy. K_{2i} — instantaneous coefficient, K_{2c} intra — cumulative coefficient calculated from intrageneration cumulative energy budget, K_{2c} inter — cumulative coefficient calculated from intergeneration cumulative energy budget

-feeding or total "physiological starvation" (praepupa, pupa), for which instantaneous efficiencies cannot be calculated, occur during the development of an individual average animal. Fig. 8B presents the course of instantaneous coefficient K_{2i}. K_{2i} in the adults, during their first 20 days of their imaginal life, reaches a level nearly up to 60%. However, the losses for R, during the praepupa and pupa stages, results in a cumulative K_{2c} (Fig. 8A) that is hardly 20% in the period immediately after transformation, it is never greater than 30–40% during the first 20 days of the adult life, and only after 200 days it attain 47%.

Terrestrial Acarina, stored-product deposit feeder — *Rhisoglyphus echinopus* (KLEKOWSKI and STĘPIEŃ, in litt.). Food — rye germs, temp. 25°C. Measured C, R, P_g, P_r. As has already been mentioned, three periods of feeding and growing (active larva, active protonympha, active tritonympha) occur in this species (Fig. 9A, B) alternating with periods of physiological starvation and loss in body weight (egg, resting larva, resting protonympha, resting tritonympha). During the imaginal period (Fig. 9C) the production of eggs per average individual is 6 times greater than the quantity of energy accumulated in the body of an average parent-individual.

In this species, two types of cumulative budgets and cumulative efficiencies were calculated. Distinguishing these types of budget is a result of the following reasoning: the fertilized eggs belong to one generation, but the cost of their production was "paid for" by the parents belonging to the previous generation. Then the cost of production of one egg is calculated from the consumption and assimilation of an average mature adult (cumulated for half of the mean imaginal life, as the mortality rate of adults in the culture was practically constant). Such a budget may be called an "intergeneration" one. If the cost of production of an egg or a young one is not taken into account, such budget may be called an "intrageneration" one. In such a species with its alternate active (feeding) and resting (starving) periods, all the instantaneous efficiencies are periodic, and can be calculated only for periods with "positive production".

The instantaneous assimilation U_i^{-1} (Fig. 9D) in *Rhisoglyphus echinopus* is very high in active larva (95%) and decreases to ca. 50% during the time of egg production. But the inter-generation U_c^{-1} has one explicit maximum in active protonympha (73%).

The instantaneous K_{1i} (Fig. 9E) varies greatly during the preimaginal development, but is always high (up to 60%), which is an evidence of how well these stages use their food during the periods of feeding in order to ensure a store of energy for the following periods of "physiological starvation". The highest value (40–45%) of K_{1c} is attained in the active protonymph and tritonymph, which means, that these are the stages which best act as "energy carriers" to the consumers of next trophic level (e.g. predatory Acarina). As high a value for K_{1c} was also found during the period of egg production.

A similar picture is given by the coefficient K_{2i} (Fig. 9F). Instantaneous K_{2i} exceeds even 80%, when both the body growth and egg production are intense. Intergeneration K_{2c} is also high because the non-feeding periods are relatively short and the loss of energy relatively small as compared with the bodies' stored reserves.

As it can be seen from the Figures 9D, E, F the intra- and intergeneration efficiencies differ considerably at the beginning of individual development,

when the "cost" of production of 1 egg is essential as compared with the energy budget of the whole animal. Later on, both types of budget and efficiencies do not differ among themselves.

Predatory crustacean, planktonic copepod *Macrocyclops albidus* (KLEKOWSKI and SHUSHKINA 1966, SHUSHKINA et al. 1968). Food — Paramecium, 1 g wet wt./m³, temp 21°C. Measured C, R, P_g up to the onset of reproduction.

As is seen on Fig. 10, U_c^{-1} decreases during the preimaginal development from more than 90% to 40%, and is analogous with K_{1c}, because K_{2c} remains constant at about 50%. Therefore, it can be assumed that food utilization is
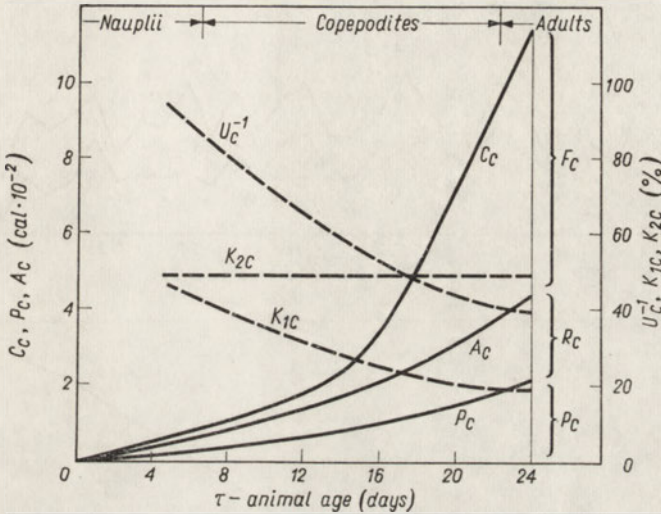
Fig. 10. Cumulative energy budget and efficiencies for *Macrocyclops albidus*, food concentration 1 g/m³, period before reproduction (compiled from data in KLEKOWSKI and SHUSHKINA 1966 and SHUSHKINA et al. 1968)

much better in the instance of young animals (nauplii and young copepodits) than in the instance of the older ones (older copepodits and adults). Similarly as in the instance of Simocephalus the younger stages are better "energy carriers" between microplankton (e.g. protozoans) and the predatory zooplankton and fish.

Predatory insect, larva of dragonfly *Lestes sponsa* (FISCHER 1967). Food — Daphnia and Tubifex; temp. 22°C. Measured C, P_g, R for the whole larval development.

As it can be seen on Fig. 11A, daily budget parameters are variable, and equally variable would be the instantaneous efficiencies calculated on this basis. However, the very same daily budget parameters in a cumulated form (Fig. 11B) give a much more uniform and stable picture. During the hemimetabolic development of *Lestes sponsa* rapid quantitative and qualitative changes do not take place in the metabolic and energy accumulation processes, as it happens in the instance of holometabolic Tribolium or in mites. The Table IV presents the cumulative budget and efficiencies for the end of larval development.

U_c^{-1} as well as K_{1c} are both rather low for predators, most probably because they were cultured in conditions of food excess. K_{2c} is high, much higher
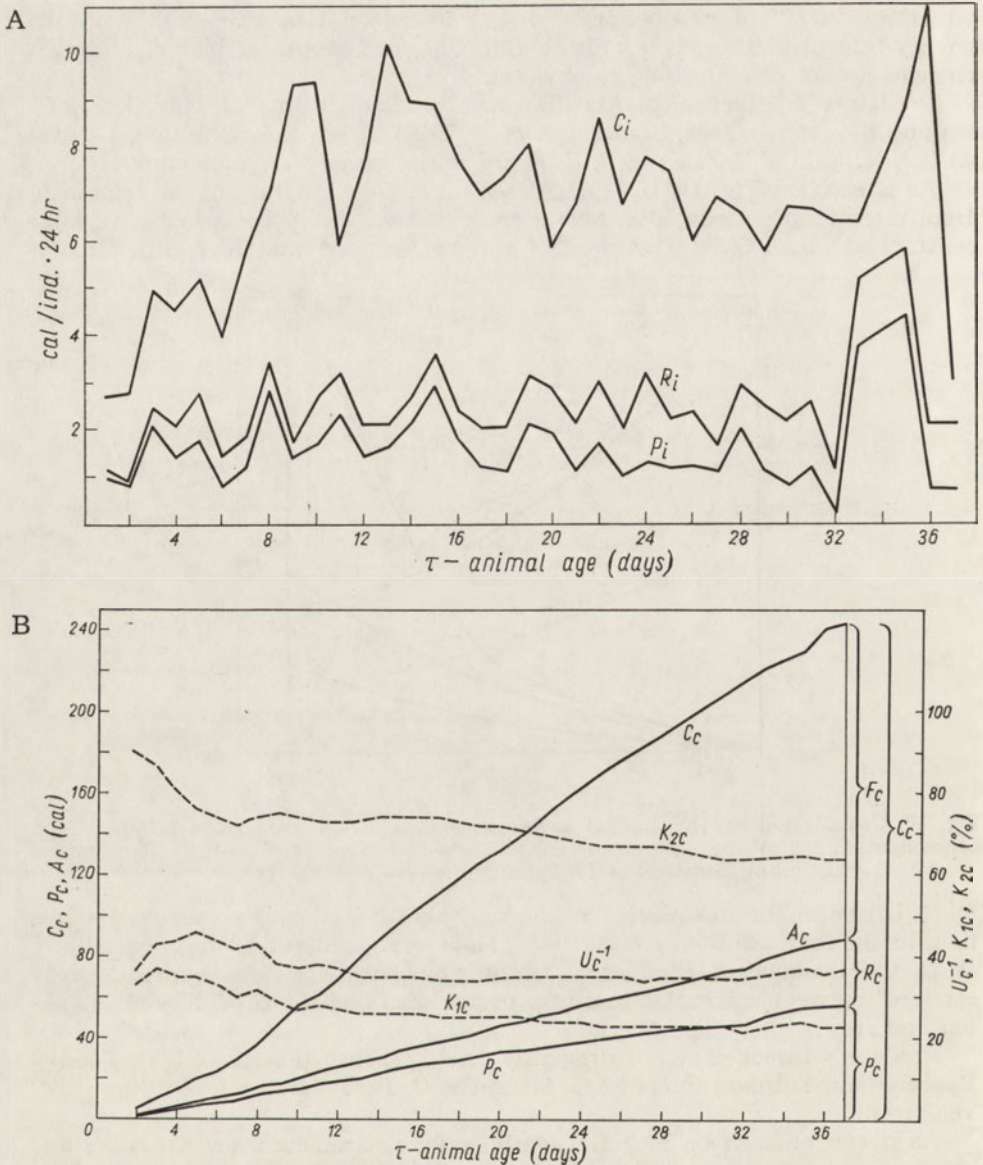
Fig. 11. Energy budget for *Lestes sponsa*; whole larval development (after FISCHER 1967). A — Changes of daily rates of consumption, respiration and production; B — Cumulative energy budget and efficiencies

than in Macrocyclops. This is probably due to the fact that Macrocyclops hunts actively, using up a great amount of energy, while Lestes lies still, waiting for the prey; its locomotive movements are minimal, especially in conditions of food excess.

Another kind of applying the idea of cumulated budget is the energy budget for generation of protozcan *Dileptus cygnus* (STACHURSKA 1969). All

Table IV. *Lestes sponsa* (after FISCHER 1967)

Animal age	$\sum\limits_{\tau_0}^{\tau_{37}}$ (cal)					%		
	C_c	P_c	R_c	A_c	FU_c	U_c^{-1}	K_{1c}	K_{2c}
Larva at τ_{37} just before metamorphosis	243.8	56.8	32.4	89.2	154.6	36.6	23.3	63.8

the budget parameters and efficiencies are calculated for an average genera-
tion time. As this protozoan divides into two identical descendant individuals,
the generation energy balance informs about the efficiencies, with which the
reduplication of the amount of energy cumulated in the bodies of animals
takes place.

Example of applying the cumulative energy budget to field population

During a course in "ecological bioenergetics", in 1968 (GRODZIŃSKI and
KLEKOWSKI [eds] 1968), the author had the possibility to discuss energy balan-
ces with the lecturers on this course: Dr A. DUNCAN (University of London)
and Dr. J. PHILLIPSON (at the time — University of Durham, at present — Uni-
versity of Oxford). The result of these discussions was an attempt to calculate
cumulative energy budget for the full annual population cycle of a Phalangid
— *Oligolophus tridens*. All the data in the individual energy budget, composi-
tion and abundance of population number of *O. tridens* from Durham surroun-
dings from J. PHILLIPSON's papers and his personal information, for which the
author is very grateful. Also the author wishes to acknowledge Dr. DUNCAN
and Dr. PHILLIPSON for their valuable assistance while calculating and discus-
sing this example of energy balance. The procedure was as following.

Out of the population data the average duration of subsequent instars
(Fig. 12A) was estimated, assuming that the following stage begins when 50%
of individuals of this population attains this stage. Then, from the data on
survivorship, number of individuals in each stage per m² (Fig. 12B) and the
average duration of instars, the participation of respective developmental
stages in successive moments of population development was calculated, and
then the elimination for subsequent instars (average per 1 m²). The cumulative
individual budget for male and female, belonging to this particular population
(Fig. 12C, D), was calculated on the basis of field data and laboratory measu-
rements of respiration and calorific value. The population production was cal-
culated from the "sum of elimination" acc. to formula (17); the remaining
parameters of cumulative budget — according to formulas of the type (19).
As T_1, T_2 ... T_n were taken the average times of transition to the next instar.

As it can be seen on Fig. 12C, D, cumulative efficiencies (U_c^{-1}, K_{2c}) are
similar in both sexes, but in the population budget (Fig. 12E) attention is
drawn to small variability of K_{2c} (about 15%) during the whole cycle and the
constant U_c^{-1} (about 40%) during the period of intensive elimination. This
small variability of the populational K_{2c} seems to confirm the opinions about
the relative constancy of this efficiency indicator within the population (WIN-
BERG 1962, 1968, SHUSHKINA 1968). We can also find out from Fig. 12E what
was the participation of both sexes and eggs in the sum of energy passed by
population to predators and decomposers. The Table V compares some of the

budget parameters of discussed population, calculated for the entire annual cycle, using both methods: from increments (formula 15) and elimination (formula 17).

Table V. Energy budget of population of *Oligolophus tridens*; Durham population

Parameters or efficiencies	cal/m² ·yr	
	Calculated by Dr. PHILLIPSON from formula (15)	Recalculated by J. P., A. D. and R. Z. K. from formula (17)
P_c	203	215
R_c	957	1145
A_c	1160	1360
K_{2c}	17.5%	15.8%
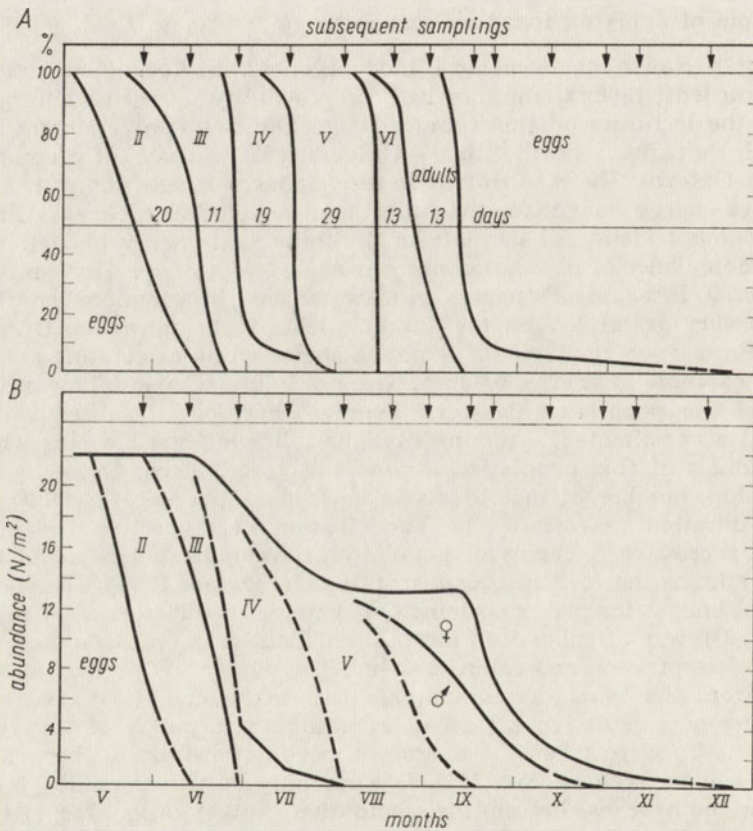
Fig. 12. Cumulative energy budget for a field population of *Oligolophus tridens* (all experimental and field data from papers of J. PHILLIPSON or calculated purposely by J. P.). A — Calculation of average duration of subsequents instars (II–VI) from population data; B — Estimation of mortality and age-instar-composition from population figures; C — Cumulative energy budget and efficiencies for an average male; D — Cumulative energy budget and efficiencies for an average female; E — Cumulative energy budget for whole year-cycle of population; calculated from "sum of elimination" (after formulae 16, 19)
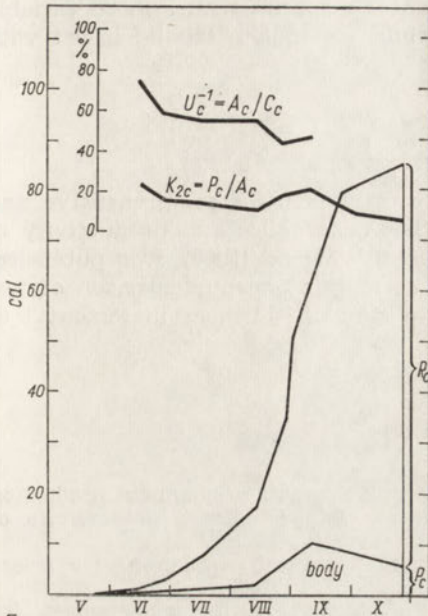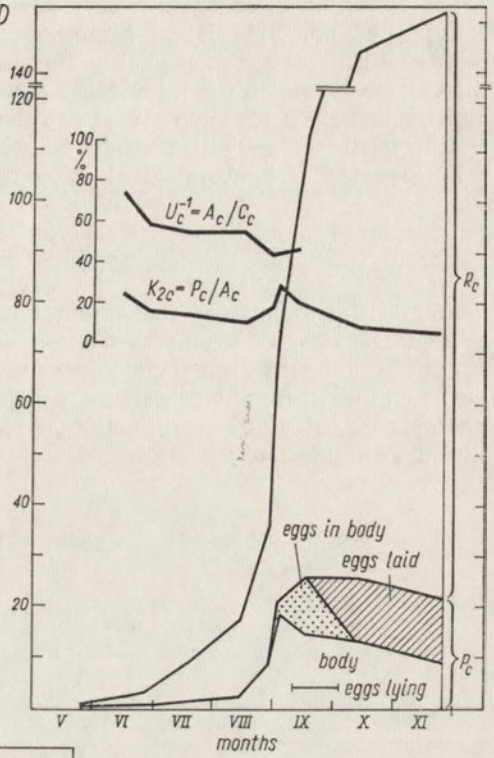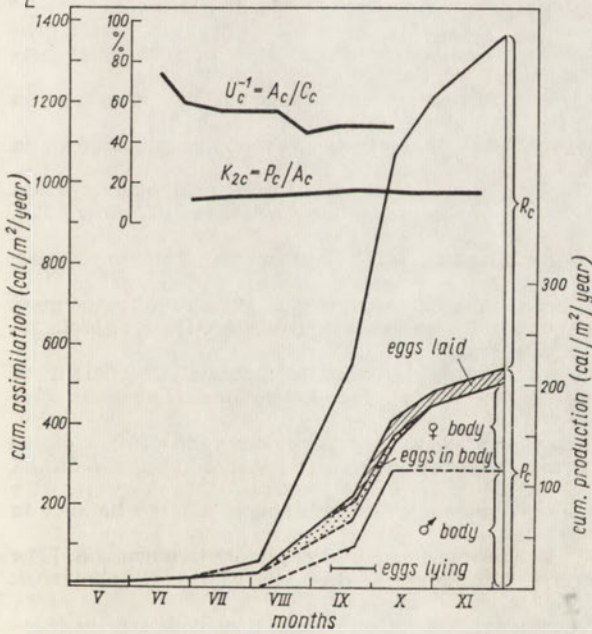
As it might have been expected since the same original data was used (comp. p. 62 and Fig. 3B), both methods gave similar results for the entire cycle (the differences are probably the result of some approximations made in the calculations). On the other hand it would be very interesting to make a similar comparison for the natural population of a species with a more variable characteristic of growth than in Oligolophus, e.g. holometabolic insect with a long period of "physiological starvation".

Addendum

While this paper for the symposium was in print, a comprehensive and excellent review of problems dealing with bioenergetics and productivity of aquatic organisms and their communities by MANN (1969) was published. Among other things it contains a similar as in this paper comparison of two methods of calculating production (from a sum of "biomass increments" or sum of "elimination").

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AN ATTEMPT TO ESTIMATE CONSUMPTION, RESPIRATION AND PRODUCTION OF *LEPTODORA KINDTII* (FOCKE) IN FIELD AND LABORATORY EXPERIMENTS

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ABSTRACT

Average daily food ration of *L. kindtii* (experiment in situ, temp. 17°C), $C = 30\%$ of its weight. Respiration (at a temp. 16°C) $R = 1.4$–11.8 ml $O_2 \cdot 10^{-4}$/ind.$\cdot 24$ hr — depending on the size. Daily increment of reproducing individuals $P = 10\%$ of their weight, assimilation $A = 87\%$ of energy consumed, energy used for growth $K_1 = 39\%$ of energy consumed and $K_2 = 45\%$ of energy assimilated. The consumption of *L. kindtii* population in July and August, may be 15–43% of the net production of Cladocera.

INTRODUCTION

Leptodora kindtii (Focke) is a common planktonic predator, the ability of which to control the zooplankton numbers is often pointed out (Hall 1964, Wright 1965). However, the data on the production of this species are very scant (Lebedev and Malcman 1967; Ščerbakov 1967) and also those on its feeding on zooplankton.

In the eutrophic Mikołajskie Lake, 100–400 ind./m³ of *L. kindtii* are found from May to September. The maximum takes place in July and amounts to 1200 ind./m³. Production of the entire population, during the period of its maximum occurrence [1] i.e. in July and August, for the layer 0–12 m (epi- + metalimnion) was 2.58 g/m³ at the average biomass 0.44 g/m³.

METHODS

Estimation of food selectivity and feeding rate on zooplankton of *L. kindtii* was made in a field experiment consisting in several hours' exposure of samples of natural zooplankton in the lake. A set of apparatus, of Gliwicz's design (1967), each of a volume 3 l was used for the experiment. Into these apparatus a different number of *L. kindtii* individuals (2–10) were introduced, of an average weight 1.28 mg. The experiment was carried out twice during August, 1968. I series lasted 7hr, the II series — 10hr. Comparison of the zooplankton

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[1] A detailed description of the occurrence, dynamics, age and size structure, method of estimating individual weight and production would be the subject of a separate publication.

numbers in exposed apparatus and control samples (average zooplankton number, from samples taken from the habitat at the beginning of experiment, was assumed as the control) and also of the species composition showed that out of the three distinguished groups of planktonic organisms: Rotatoria, Cladocera and Copepoda, most intensively were eaten adult Cladocera individuals (*Daphnia cucullata*, *D. longispina*, *Chydorus sphaericus*), were the losses amounted to 50% of the control state. But no differences were found in the numbers of Rotatoria and Copepoda avoided by *L. kindtii* probably because of their small size (Rotatoria) or great mobility (Copepoda).

Respiration of *L. kindtii* was measured in 25 ml bottles with lake water filtrated through bacterial filter. The experiment was carried out at a temp. 16°C. Two series of samples were carried out: I series — constant number of individuals at a variable exposure time (3–24hr), II series — constant exposure time at a variable number of individuals (1–10), in the I, II and III development stages, and mature individuals.

As comparative data were assumed those obtained by theoretical calculations of respiration rate of *L. kindtii*, applying the WINBERG's formula (WINBERG 1950, BELJACKAJA 1959) for the dependence between respiration and the animal's weight, valid for all fresh-water crustaceans (temp. 20°C)

$$R = 0.105 \cdot W^{0.81}$$

where: R — respiration in ml $O_2 \cdot 10^{-4}/hr \cdot ind.$,
W — weight in g of fresh weight.

Results of own experiments were adjusted to the temp. 20°C, acc. to corrections of Krogh's curve.

RESULTS

Food ration

The amount of food eaten during 24hr, daily food ration, was expressed as the per cent of the average weight of exposed *L. kindtii* individuals. The weight of eaten cladocerans was determined acc. to MORDUHAJ-BOLTOVSKOJ (1954). Both at 7-hr and 10-hr exposure the greatest daily food ration, equal to 40–48% of body weight, took place at a density 4–5 *L. kindtii* ind./apparatus (Fig. 1), which corresponds with the maximum number of this species found in Mikołajskie Lake: about 12 ind./10 l. In both these experiments, at smaller as well as greater densities the feeding rate decreased (Fig. 1).

The smallest number of individuals used in the experiment was 2, which corresponds to the density about 7 ind./10 l. Average density of *L. kindtii*, in summer, was about 3 ind./10 l, which would correspond to the density equal 1 ind./apparatus. Therefore in order to obtain an approximate information on the feeding rate of *L. kindtii*, at its average density in the habitat extrapolation was applied (Fig. 1), and the value of 30% was obtained. Thus the range of daily food ration of *L. kindtii* is 30% of its weight at its average number, and up to 48% at its maximum number.

Respiration

The curves of the dependence between respiration rate and size of individuals (at a temp. 20°C) obtained experimentally and calculated have a similar course (Fig. 2). However, the results obtained after 3 and 6-hr exposures

Fig. 1. Changes of daily food ration of *L. kindtii* (as % of its body weight) at its different density in the apparatus. Exposure time: 1 — 7hr; 2 — 10hr
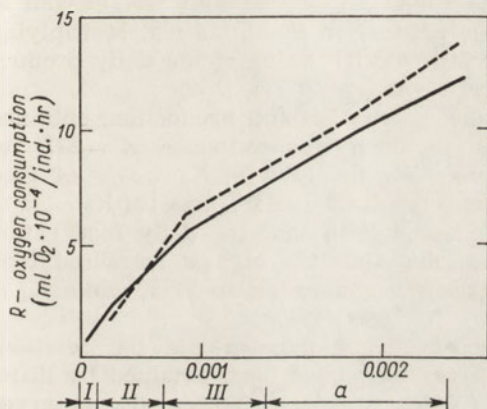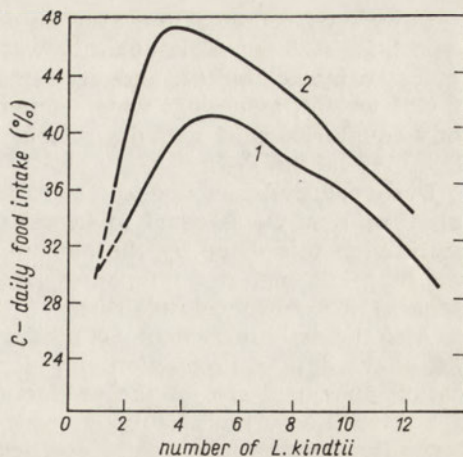

Fig. 2. Dependence between the respiration rate of *L. kindtii* and the weight obtained in the experiment (——) and calculated according to the formula: $R = 0.105 \cdot W^{0.81}$ (- - -) I, II, III — successive development stages; a — mature

should be eliminated as too high, and so the results obtained at the maximum density (in the experiment) — as too low.

Thus, for respective development stages (size classes) the respiration rate, at a temp. 20°C has the following values (ml O_2 10^{-4}/ind.·hr): I — below 1.4; II — 1.4–4.8; III — 4.0–8.0; mature individuals — 7.5–11.8. The results obtained by WINBERG (1950) are of the same magnitude (3 ml $O_2 \cdot 10^{-4}$/ind.·hr).

Assimilation and growth efficiencies

Out of the daily food ration measured in the field experiment, and respiration measured in the laboratory experiment and net production of *L. kindtii* — calculated out of field data, the coefficients among these parameters were calculated, after converting them into calories. The coefficients were calculated only for individuals of an average weight 1.28 mg, because only for this class of size the daily food ration was determined. This is the average weight of individuals in the III stage (between the 2nd and 3rd molting) and mature individuals in periods of occurrence of *L. kindtii*. The participation of this class of size of animals was 70%, and in the biomass 50% of the entire population.

Daily food ration at the average density of *L. kindtii* is 30% of its body weight, i.e. 0.38 mg. This quantity was lowered some 15% i.e. by chitin parts not eaten by *L. kindtii*[2], and the remainder was multiplied by 0.46 cal/1 mg of wet weight, assuming: water contents 90%, calorific value of cladocerans' body equal 4600 cal/1 g of dry weight (WINBERG 1968). Thus daily food intake $C = 0.147$ cal/ind.·24hr.

Daily energy losses due to respiration were obtained by assuming the equivalent of 1 ml O_2 as equal to 4.8 cal (KLEKOWSKI and SHUSHKINA 1966a) and multiplying this value by the amount of oxygen consumed by an individual weighing 1.28 mg, at a temp. 16°C. Thus the daily respiration (cost of maintenance) $R = 0.070$ cal/ind./24hr.

Also the daily increment, i.e. production was also converted to energy units. Out of the data of production and biomass of individuals of the III stage and mature ones, and also of the production and biomass of eggs, in the months cf *L. kindtii* occurrence (July, August), for epi- and metalimnion (temp. 17°C), it results that the mean daily coefficient P/B for these two stages and eggs is about 0.1. That is the daily production is about 10% of body weight, and so for an individual weighing 1.28 mg the production $P = 0.128$ mg. Multiplying this last value by 0.46 cal/1 mg wet wt. a calorific value of the daily production was obtained equal to 0.058 cal/ind.·24hr.

From so calculated daily food intake, respiration and production, obtained by different methods the assimilation of food was estimated $A = 87\%$ of food intake, efficiency of food utilization for the growth, $K_1 = 39\%$ of food intake, and efficiency of assimilated energy utilization for growth, $K_2 = 45\%$. These numbers are resulting from an assumption that the daily food ration is equal to 30% of body weight. Assuming thus the highest measured food ration i.e. 48% of body weight — A is lower and equals to 54%, while $K_1 = 24\%$.

The above mentioned parameters of energy balance and the relations among them seem to be reliable, however they have been obtained by different approaches. Daily food ration of 30–50% order has been also observed among other predators, e.g. mature cyclops (SHUSHKINA 1964; KLEKOWSKI and SHUSHKINA 1966a,b; SHUSHKINA and KLEKOWSKI 1968). Considerably high food assimilation of 70–90% order was observed both in case of the already mentioned cyclops and some filtering cladocerans and copepods (SUSHCHENYA 1963; PECEN and KUZNECOVA 1966; OSTAPENYA et al. 1968; TSIKHON-LUKANINA et al. 1968) in lower food concentrations. On the other hand the K_2 value of 40–50% order, obtained here, seems to be frequently observed for the naturally reproducing populations of various aquatic organisms, judging by the comparison of these data by SUSHCHENYA (1963) and SHUSHKINA (1968).

Utilization of Cladocera production

Having the data on food ration of the investigated stages of *L. kindtii* and by comparing them with the production of cladocerans it can be approximately estimated, which part cf this production is eaten by individuals of the III stage

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[2] *L. kindtii* is a predator, which sucks out the contents of the prey (SEBESTYEN 1951, MORDUHAJ-BOLTOVSKAJA 1960); per cent of chitin in the weight of cladocerans was assumed as equal of 15% (*Žizn Presnyh vod*, 1956).

and mature *L. kindtii* individuals (assuming that their average daily food ration is 30% of body weight, i.e. 0.38 mg/ind.). Average number of both these stages, in July and August, was 190 and 195 ind./m^3, respectively. That is the total mass of consumed food was 2.17 in July and 1.08 g/m^3 — in August. As the estimation of cladoceran production was not available during the period of investigating on the feeding of *L. kindtii*, therefore the data from earlier investigations (1963, 1964) were used (HILLBRICHT-ILKOWSKA and WĘGLEŃSKA 1970 — modified data). In those years cladoceran production was jointly for epi- and metalimnion in the months of July — 13.8 g/m^3 and 6.4 g/m^3, and in the months of August: 4.4 g/m^3 and 2.5 g/m^3. Therefore the consumption of mature *L. kindtii* population is 15–43% of the production of its prey, i.e. that such per cent of net cladoceran production may be utilized by their predator in summer months. This value is close to the one estimated by HALL (1964) and WRIGHT (1965), who say that *L. kindtii* may eat 25–35% of net production of Daphnia population.

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SOME PROBLEMS DEALING WITH ENERGY PROCESSES OF *CERIODAPHNIA RETICULATA* (JURINE)

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ABSTRACT

The average twenty-four hours' increase, reproduction intensity and the growth rate of young individuals of *Ceriodaphnia reticulata*, fed in cultures with four algae species, increase together with an increase of the calorific value. However the death rate during the juvenile period decreases at the simultaneous speeding up of maturation and lengthening of the life period and the reproduction period.

Ryther (1954), Vasileva (1958), Slobodkin (1959), Czeczuga (1960), Kryuchkova (1967), and several other authors were interested in the dependence between the quantity and quality of available food and the growth and reproduction intensity of zooplankton. It has been found during those investigations that the growth rate, time in which maturity is achieved, fertility and the life length are quicker and greater, when the food is more valuable. Consumption of food by planktonic animals and their condition were the criteria of food value. Only Kryuchkova (1967) linked her studies on *Moina rectirostris* Leydig with the calorific value of algae used in the experiment.

Ceriodaphnia reticulata, cultured in laboratory conditions were fed with the following algae species: *Chlamydomonas nivalis* Wille, *Chlorella vulgaris* Beyer, *Chlorella ellipsoidea* Gerneck, *Ankistrodesmus falcatus* var. *duplex* Kütz.

The increment and death rate of *C. reticulata* in the juvenile period and the intensity and rate of reproduction were investigated from the moment of maturity till death. Apart from that, the calorific value of the above mentioned algae was determined. Combustions were made in the calorimeter microbomb in the Nencki Institute of Experimental Hydrobiology, Polish Academy of Sciences[1]. The results obtained are presented in Table I. Taking into consideration the amount of calories obtained after the combustion of 1 mg of dry weight of respective algae species and the proportional contents of mineral compounds, no visible relation and no distinct influence can be noticed on the increase and time of reproduction of *Ceriodaphnia reticulata*. It has been observed that in the instance of feeding with *Chlorella vulgaris* algae, where the content of mineral compounds is the lowest, maturity is attained at the

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Table I. Growth, death rate and reproduction rate of

Food	Number of samples	Number of individuals	Calorific value of dry weight (cal/g)	Ashes (%)
Chlamydomonas nivalis Wille	18	50	2.76	11.2
Chlorella vulgaris Beyer	38	96	2.98	7.2
Ch. ellipsoidea Gerneck	38	109	2.41	22.8
Ankistrodesmus falcatus var. *duplex* Kutz	13	39	5.53	23.5

latest and the death rate in the juvenile period is the highest (28–60%, average 46%).

From the point of the calorific value of respective algae species used in our experiments they can be divided into two groups: 1) less calorific — *Chlamydomonas nivalis*, *Chlorella vulgaris* and *Ch. ellipsoidea* (2.4–2.98 cal/g of dry weight; 3.1–3.3 cal/g of organic compounds) and 2) more calorific — *Ankistrodesmus falcatus* var. *duplex* (3.5 cal/g of dry weight; 4.61 cal/g of organic compounds). So, while feeding with algae from the first group the growth rate of young individuals to the moment of maturation is on the average 2.3––3.1 μ/hr, in case of individuals fed with *Ankistrodesmus falcatus* it is 5.5 μ/hr. Therefore *Ceriodaphnia reticulata* fed with more calorific food attains maturation after 72hr, while in the first group, less calorific, after 96hr. Some *C. reticulata* individuals fed with more calorific food with a large amount of fat balls contain more embryos in the broach cell (6–8). Individuals fed with less calorific food are pale, and 2–4 embryos usually develop in the broach cell, sporadically 6, and not all of them are strong enough to survive.

The calorific value of food affects the fertility and the length of the reproduction period. At less calorific food the average reproduction period is 13––17 days, and the average fertility of female is 10–18 young ones. On the average, the period of reproduction is lengthened to 19 days, and the average number of young ones increases to 32 individuals, when feeding with more calorific food.

Comparing those two food groups, it is easily noticed, that in case of less calorific food the number of *C. reticulata* attaining maturation varies (40–90%) at a large range of death rate in the juvenile period (10–60%). When feeding with more calorific food the death rate is low (10–15%), and 85–90% individuals attain maturation.

These are the average results, as the range of individual samples was often quite big. In autumn and winter the divergence of results was greater than in spring and summer, despite the fact that the temperature was maintained within 22–24°C and artificial light was applied. The age of the algae culture used for feeding and the conditions, in which the parental individuals were cultured, had also an effect on the range of variations. The growth of individuals was more visible or the fertility was better and the reproduction period was longer after transfering the individuals from worse food conditions into better ones. When applying various food concentrations the best results were obtained at average concentrations. At very low and very high concentrations the death rate increased giving thus very different results.

Ceriodaphnia reticulata reared on different algal food

Calorific value of organic compounds (cal/g)	Average increase (μ/hrs)	Death rate in the juvenile period		Length at the moment of maturation (μ)	Length of reproduction period	Average number of young ones per 1 mature individual
		%	Average			
3.12	2.3		40	563	13	10
3.22	2.8	28—60	46	605	16	13
3.36	3.1	8—32	20	584	17	18
4.61	5.5	10—15	13	597	19	32

Figure 1 presents the reproduction intensity of *Ceriodaphnia reticulata* fed with various algae species. The results are given in per cents in relation to the total number of young individuals born of individuals fed with different food. The entire reproduction period was divided into 3 periods (±5 day intervals) i.e. initial, middle and final period of reproduction. As it can be seen, the
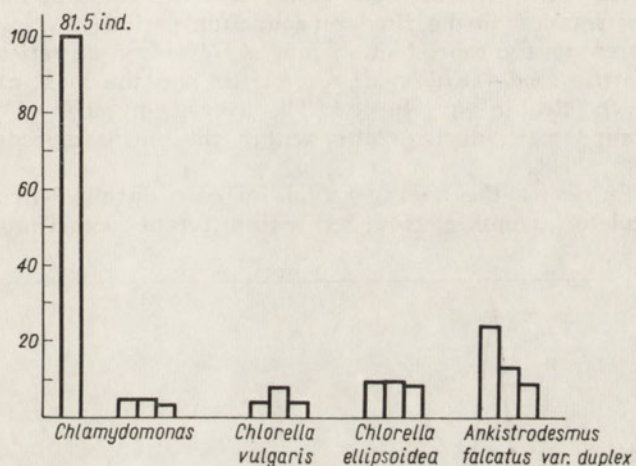

Fig. 1. Reproduction intensity of *Ceriodaphnia reticulata* fed with different algae species

reproduction rate in the first two periods is identical, with a slight decrease in the final period, when feeding with *Chlamydomonas nivalis* algae. *Ceriodaphnia reticulata* fed with *Chlorella vulgaris* algae reproduces most intensively in the middle period. When feeding with *Chlorella ellipsoidea* algae, the reproduction rate is similar as when feeding with *Chlamydomonas nivalis*, but the average fertility is twice as big. When feeding with *Ankistrodemus falcatus* var. *duplex* algae the most intensive reproduction takes place in the first 5 days, in the middle period the intensity decreases almost 50%, and it drops further in the final period.

Figure 2 illustrates also these results. The reproduction periods are here pointed out. The algae species are arranged according to the increasing calorific value, calculated per 1 mg of organic compounds. The average fertility
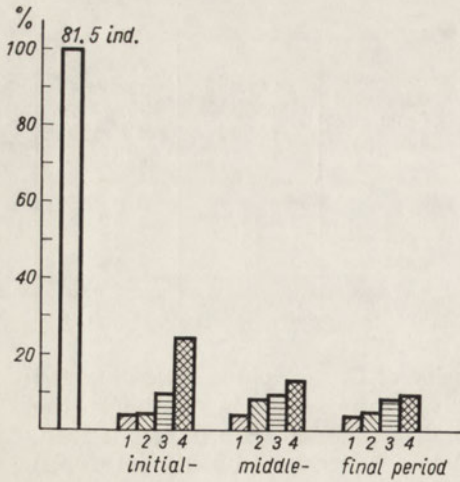
Fig. 2. Changes in the reproduction intensity of *Ceriodaphnia reticulata* (in three reproduction periods) fed with different algae species. 1 — *Chlamydomonas nivalis*; 2 — *Chlorella vulgaris*, 3 — *Chlorella ellipsoidea*, 4 — *Ankistrodesmus falcatus* var. *duplex*

increases together with the increase of the calorific value of food. The differences are the smallest in the final reproduction period.

Figure 3 presents the reproduction rate of *Ceriodaphnia reticulata* fed with the least calorific food — *Chlamodynas nivalis* and the most calorific one — *Ankistrodesmus falcatus* var. *duplex*. The average number of young individuals from one female, during 24hr, within the entire reproduction period, are given.

Figure 4 illustrates the average total increase during 24hr (μ) of *Ceriodaphnia reticulata* (juvenile period) fed with different food. The greatest diffe-
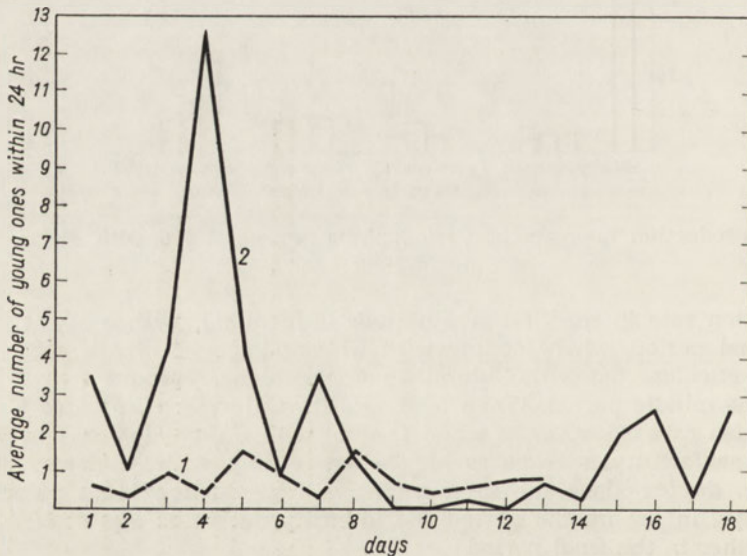

Fig. 3. Reproduction rate of *Ceriodaphnia reticulata* fed with the least calorific food: 1 — *Chlamydomonas nivalis*, and the most calorific one: 2 — *Ankistrodesmus falcatus* var. *duplex*
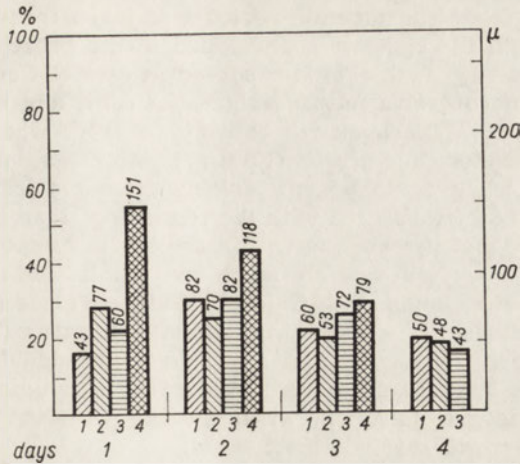
Fig. 4. Average total increase within 24hr of *Ceriodaphnia reticulata* fed with different algae species. $100^0/_0 = 273$ μ = average total increase of the individual i.e. average length of females at the moment of attaining maturation minus average length of young ones immediately after the birth. 1 — *Chlamydomonas nivalis*, 2 — *Chlorella vulgaris*, 3 — *Chlorella ellipsoidea*, 4 — *Ankistrodesmus falcatus* var. duplex.

rences in the increase, depending on the kind of food, are noticed in the first and second day of the juvenile period. The most intensive increase takes place, when feeding with *Ankistrodesmus falcatus* var. *duplex* algae. The increase is more or less even on the third and fourth day. There is no visible effect of the kind of food, and in some *Ceriodaphnia reticulata* individuals the broach cell becomes more protruded and also other symptoms of approaching maturation may be observed.

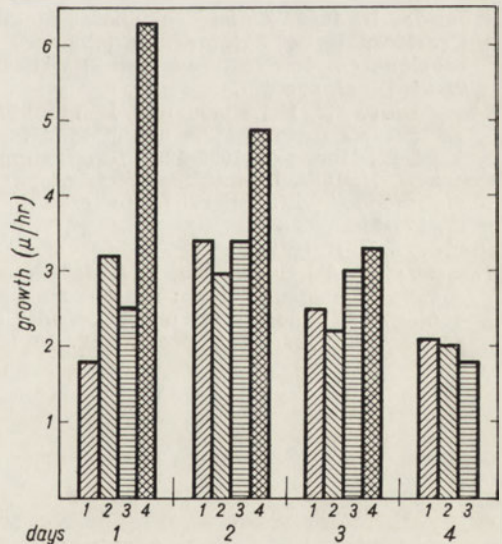Figure 5 presents the average growth rate of respective individuals (μ/hr)

Fig. 5. Average increases (μ/hr) every 24hr of the juvenile period of *Ceriodaphnia reticulata*. 1 — *Chlamydomonas nivalis*, 2 — *Chlorella vulgaris*, 3 — *Chlorella ellipsoidea*, 4 — *Ankistrodesmus falcatus* var. *duplex*

fed with different food. The juvenile period was taken into the consideration, to the moment when the eggs were developed in the broach cell. During the first 24hr the greatest growth rate is observed in case of *Ceriodaphnia reticulata* fed with *Ankistrodesmus falcatus* algae (6.3 μ/hr) and *Chlorella vulgaris* algae (3.2 μ/hr). The smallest growth rate is observed, when the individuals are fed with *Chlamydomonas nivalis* (1.8 μ/hr). After 48hr, the growth rate is still the greatest, when feeding with *Ankistrodesmus falcatus* (4.9 μ/hr). In case of *Ceriodaphnia reticulata* fed with the remaining algae species the growth rate is very similar and its range is within the limits 2.9–3.4 μ/hr. After 72hr, the differences in the growth rate are much less visible, and the lowest growth rate is that of individuals fed with *Chlorella vulgaris* algae (2.2 μ/hr) and the greatest of individuals fed with *Ankistrodesmus falcatus* (3.3 μ/hr). During that time the majority of *Ceriodaphnia reticulata* individuals fed with *Ankistrodesmus falcatus* are already mature. After 96hr (excluding the individuals fed with *Ankistrodesmus falcatus*), when feeding with the three remaining algae species, the growth rate is almost equal.

The following conclusions can be reached:

1. Out of four algae species used in the experiments, *Chlamydomonas nivalis* is the least valuable one, while *Ankistrodesmus falcatus* var. *duplex* is the most valuable one.

2. Together with an increase of the calorific food value an increase of the average growth during 24hr and the growth rate of young individuals (μ/hr), and an increase of the reproduction intensity may be observed.

3. Together with an increase of the calorific food value the death rate in the juvenile period decreases, and the maturation is quicker. Also the reproduction period is lengthened, and by the same the life span of respective individuals.

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PRIMARY PRODUCTION AS A SOURCE OF ENERGY IN AQUATIC BIOCENOSIS

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ABSTRACT

The basic problem of production line in limnology was discussed, that may be reduced into the question of magnitude and cost of production of a given type of organic matter in water bodies. The studies on the energetical budget of organisms and biocenoses in ecology and geophisics bearing upon different assumptions lead to inconsistent results, since they do not make allowances for high complexity of organims-habitat relations. The limnologists are interested in ecological efficiency of primary production. Discrepancies have been found between the calorific value of aquatic plants evaluated from their chemical composition and that determined with a bomb calorimeter.

We are celebrating the 50th anniversary of the Nencki Institute of Experimental Biology — the Institute with which Polish hydrobiology is strongly connected from its very beginning.

However our symposium has a working character, the anniversary celebration allows to present some round figures of a more general meaning. Next year it will be a hundred years from the edition of the first limnological treatise, by Forel, a father of limnology. Year ago 80 years has passed since the concept of "plankton" and parallel the one of "productivity" (Hensen 1887) were introduced into hydrobiology.

Hensen was the first to outline the scheme of the circulation of matter. Apstein (1896), Hensen's coworker, introduced to planktonology concepts of "producer" and "consumer". Since then the problem of biological productivity become well established in hydrobiology, and the symposium is dealing with this type of problems.

I do not want to discuss the historical development of these ideas, but I would like to underline that the tempestous development of the whole idea is expressed by the two basic problems. How much of the determined organic matter is produced in water reservoirs, and the cost of this production. All problems ccncerning production have developed from these two basic ones.

Relatively early an attention was paid to the components limiting production, their circulation was investigated and their balances in water reservoirs were made. A little later an attention was directed to the energetics of various

limnological processes, and the trials of estimation of energy balances were started soon.

Since then various subjects and problems become entangled as a result of similar methodology (balancing) and terminology. On one hand it means an energy (read thermical) balance of a reservoir — a subject of interest for geophysicists and meteorologists and on the other — the energy involved in biological processes on both levels of an individual and population.

Therefore, as it is scmehow in between two different sciences (here geophysics and ecology), significant misunderstandings may occur as a result of similar terminology.

GATES (1962) in his book *Energy exchange in the Biosphera* gives the equation balancing the energy of the earth surface

$$S+R+LE+G+C+s = 0$$

further on he says "for a living organism the components are basicaly the same, only the coefficients determining the body surface are slightly different, therefore an organism should not be treated as an absolutely black body, but as a gray one". After the introduction of these corrections GATES gives an equation

$$S-(r+t)S+er+LE+G+C+s+P+M = 0$$

The last two components of this equation are new, and they are: P = photosynthesis, and M = basic methabolism. Therefore if the body temperature is constant, the photosynthesis is equal to the basic methabolism, but after all, plants are growing and produce organic matter, and as the animals do not photosynthetize, they should have a methabolism equal 0.

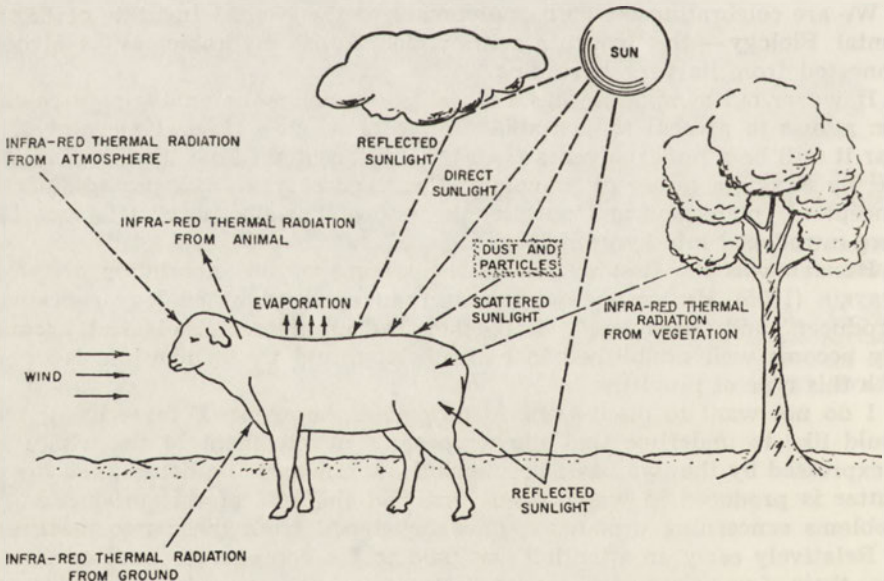Figure 1, given after GATES (1962), showing the schematic energy balance

Fig. 1. Energy exchange for an animal in a natural environment (after GATES 1962)

of an animal in the natural environment does not take into account the animal's food as a source of energy.

This point of view is not unique one, as the first of the already mentioned equations appears in various modifications in papers from the Symposium on metodology of plant eco-physiology in Montpellier, published in 1965.

This problem was most precisely analysed by BAUMGARTNER (1965). He presents a detailed energy balance of a plant community. These data show that the energy assimilated due to photosynthesis is about 1 per cent of the energy used for evaporation, or in a different calculation a quantity of 90 g of water is evaporated per 1 g of assimilated CO_2 (for the white beet), and respiration is equal to 23% of gross assimilation. In effect, for the prcduction of organic matter 1 to 2 $mcal \cdot cm^{-2} \cdot min^{-1}$ of the leaf surface is used (solar constant — 1.98 $cal \cdot cm^{-2} \cdot min^{-1}$). In the first days of July, young fir forest at an energy balance 658 $cal \cdot cm^{-2} \cdot day^{-1}$ has an assimilation lower than 1 cal (BAUMGARTNER 1965).

Taking all this into consideration the lack of food energy on GATES' figure should be treated rather as an excessive simplification, but not as an error.

In 1968 GATES in his paper under the same title as his book (GATES 1968) gives a basic equation of the energy flow among the organism and the environment:

$$Q_{abs} = \varepsilon \sigma T_l^4 = c - LE \pm M$$

where M = basic metabolism "which for many plants can be neglected or can be included in the Q_{abs} term".

On the other hand an ecologist-physiologist analysing the bioenergetics of life processes is not interested in the radiation balance, assuming that the whole energy has its source in food (PRUS 1968).

However, the process of photosynthesis, together with its energy side, is very significant and decisive for the whole life processes on the Earth, it is only a negligible part of the radiant energy stream reaching the Earth's surface. When investigating the energy balance of the Earth's surface the quantities associated with photosynthesis are smaller than the error.

The utilization of PhAR can be then estimated not from the measurements of elements of the energy balance, but indirectly. On one hand these are investigations of the quantum efficiency of photosynthesis (investigations of WARBURG and his school), and cn the other — the energy side of primary production processes is estimated on the basis of analyses of changes of components taking part in photosynthesis (CO_2, O_2, an increase of the quantity of organic matter), and with the help of suitable coefficients an energy aspect of this process is estimated.

Quantum efficiency of photosynthetic process is not yet univocaly estimated. The obtained results vary within a broad range. WASSINK (1968) in his review of literature gives 4–10 quants/molecule of CO_2. CLAYTON (1966) established the quantum efficiency of photosynthesis as 8 quants/molecule of CO_2.

The quantum efficiency is a measure of physiological processes of photosynthesis, however, it cannot be applied for the estimation of primary production and the increase of energy in plant mass.

That is why in the ecological practice the attention is directed mainly to parameters characterizing the production of organic matter and the increase of biomass.

Having thus obtained results, the efficiency of primary production is de-

termined (0.1–2.0% utilization of PhAR — Wassink 1968 for the land; 0.05––2.14% — Pyrina 1967, Volga River; 0.102–0.416% — Mokiewskij et al. 1964 for Belorussian Lakes; 0.12–0.91% — Kajak 1970 for Mazurian Lakes).

However, since the bioenergetics of producers is nearly a negligible part of their total energy balance, the analyses of PhAR utilization give limited possibilities for conclusions.

Lieth (1968) discussing the ecological efficiency combines various possibilities of an interpretation, which are found in literature:

1) Radiation can be referred to the following units of time: a) time between the two periods of cropping (used to determine the maximal efficiency), b) full growth period (used for a comparison of efficiency of various species), c) a year (used for comparison of various places on our globe).

2) The radiation values can be given for: a) total radiation, b) its photosyntheticaly active part (visible, i.e. short-wave radiation).

3) The calorific value of plant biomass can be calculated for: a) total gross primary production, b) total net primary production, c) only for the plant parts over the ground, d) only for the crop.

4) Some of the data used for calculations are obtained with the help of coefficients: a) total radiant energy is assumed to be a double quantity of the visible energy, b) calculations of the biomass into the number of calories is based on the coefficients 4.0 or 4.5 kcal/g dry weight.

Much more is obtained from the measurements of production and the calorific values of biomass. This would be the subject of my further discussion.

The calorific value of plant material is not fully known yet, however a lot of data are now available.

Straskraba (1968) compiled materials dealing with aquatic plants. From these materials a calorific value of dry weight was calculated for species, which were also analysed in our laboratory.

Not all groups of plants have the same calorific value (Table I). From the Straskraba's data it results that the highest values are those of the plants with floating leaves — 4010 cal/g dry weight (4770 cal/g organic matter). The lowest values are those of submerged plants — 3620 cal/g dry weight (4580 cal/g organic matter). The calorific value of emergent macrophytes is similar to that of plants with floating leaves, and is 1950 cal/g dry weight (4480 cal/g organic matter). Low calorific values of submerged macrophytes,

Table I. The calorific value of macrophytes for 1 g dry weight

Species	From Straškraba. Calculated per dry weight	Our measurements of calorific values (made by Grabowski)
Acorus calamus	3660	3059—3928
Equisetum	3900	2857—3499
Phragmites communis	3870—4200	3330—4791 leaves
		3412—4753 stems
Scirpus lacustris	4000—4375	3239—4134
Typha angustifolia	3880—4160	3191—3921
Typha latifolia		3576—3879
Chara sp.	1913—2080	800—1130
Lemna sp.	3600—3750	1782—1881
Stratiotes	3340—3820	1167—1181
Polygonum amphibium	4450	2496—4080

with relatively high calorific value of their organic matter are probably a result of less precise measurements of their ash content. These plants are often strongly incrustated. The not well removed incrustation is often calculated as the inorganic matter of plant biomass. In STRASKRABA's comparison, e.g. Charales are characterized by the ash content 30–70%. STRASKRABA discussed this problem mainly on the basis of works by WESTLAKE (1965) and WETZEL (1960).

It is interesting in the STRASKRABA's comparison, that the range of variations of calorific values of submerged plants is larger (4165–5140) than for the other groups of plants (4207–5140 cal/g organic matter). LIETH (1968) decided upon 4000 cal for green terrestrial plants and for trees — 4700 cal/g dry weight.

In this place one should discuss the units to which calorific values are referred to. These values are expressed as a number of calories per gramme of organic matter, or as a number of calories per gramme of dry weight. In bioenergetical papers either a chemical compound of food is characterized, or food with minerals which are a ballast material from the bioenergetical point of view. That is why in such cases it is better to give the calorific value of all food, i.e. its dry weight, and not of a part of it, i.e. organic matter. From this point of view it would be the best to refer to the calorific value of the fresh weight of food, as fresh food is caught, swallowed, possibly disintegrated and digested.

For example an animal feeding on Charales, in order to obtain 4450 cal, i.e. to consume an equivalent of 1 g of organic matter must take 11 g of fresh weight of this plant (calculated on the basis of STRASKRABA's materials) assuming a 100% assimilation. The whole process of assimilation of energy must be adapted to turning large quantities of plant mass.

The opinions concerning this matter are not uniform, and the values are always calculated from one unit to the other. At present the calories should not be used, and the energy should be presented in joules and watts.

STRASKRABA calculated the calorific values of macrophytes on the basis of chemical analyses and various coefficients. The direct measurements done in our laboratory gave, as a rule, lower results than these given by STRASKRABA. ŁAWACZ (unpublished data) encountered a similar phenomenon during his investigations of seston calorific value.

The order of these differences in respective ecological groups of plants is quite interesting. The calorific values of plants with floating leaves do not differ almost from theoretical values, emergent macrophytes have generally a calorific value 7% lower than the theoretical one, but in case of submerged macrophytes this value is not higher than 40% of the theoretical value. These results are not numerous enough to drow some more important conclusions. The reasons of the mentioned dependence will be a subject of further investigations. Generally speaking, the bioenergetic investigations based on material obtained from the chemical composition and coefficients may lead to some serious divergences of results.

We do not have data on the plankton calorific values for our waters. The literature data — 4500–5500 cal/g organic matter (WINBERG 1960), or 6000 cal/g organic matter — (STRASKRABA 1968) should be, according to the above, treated very carefully, especially as a similar ecosystem — periphyton, also formed by algae, has positively lower values.

Calorific values of periphyton are known to a certain extent (Szczepański 1968). These values are within the limits of 550–3750 cal/g dry weight, the most frequent results are between 1000–1500 cal/g dry weight. These low values are the result of an accumulation in periphyton of large quantities of inorganic compounds, mainly of $CaCO_3$ from an incrustation. Periphyton contains usually 45–50% of organic matter. The organic matter itself has also low calorific values, most frequently 2500–3000 cal/g organic matter.

The material of Szczepańska on the seasonal dynamics of periphyton of some Mazurian Lakes is now in preparation. The calorific values of periphyton are fairly constant during the season. The biomass of periphyton is, however, increasing thus the total calorific value for the unit of area of the substratum. Changes of quantities and calorific values of periphyton are shown on the example of Lake Śniardwy (Fig. 2).
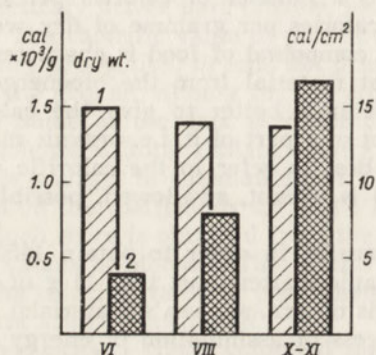

Fig. 2. Changes of periphyton abundance (1) and of its calorific value (2) in Lake Sniardwy (after unpublished data of Szczepańska)

The calorific value of this material — 1427 cal/g dry weight, is within the limits for Suwałki Lakeland — 100–1500 cal/g dry weight.

The other source of organic compounds is the allochtonous matter which supplements the primary production in reservoirs. Its share in the organic matter balance may be so big, that some reservoirs are supplied with allochtonous organic matter. This matter originates from the detritus brought in by inflows, organic litter falling on the water surface, and the detritus washed by rains from the direct drainage area. Leaf litter from the trees and shrubs on the shore is one of the sources of this matter. The importance of this source depends on the area of reservoir and the degree of its shore line development. For Lake Mikołajskie the leaf litter for 1 m of the shore line is 0.5 kg per year, a fraction of one percent of the lake production (Szczepański 1965). Levanidov (1949) determined the calorific value of leaf litter as 3500––3900 cal/g dry weight. Our results — 4835 cal/g dry weight are then considerably higher.

The gross primary production and the net primary production are the two values used in the production investigations, which can not be directly compared among themselves. As for the macrophytes, the net production is mainly used, while for algal production — the gross value. That is why it is difficult to compare the significance of these two groups of plants in the energy balance of a reservoir, and generally the comparison is an approximate one.

It is usually assumed for macrophytes that the maximal biomass is an equivalent of the primary net production (Westlake 1965). It is also assumed,

and in a rather arbitrary way, that the energetic demand of plants is 25–33%
of net production, which means that gross production is 1/4 to 1/3 higher than
net production. On this basis the ecological efficiency of PhAR is also calcula-
ted. For annual plants with a reduced root system the problem is relatively
simple. It is much more difficult to analyse in such a way the perennial macro-
phytes, as the mass of their root system can be several times larger than the
mass of aerial parts. For the reeds the ratio of the aerial shoots to the roots and
rhizomes produced during the same time is 1 : 2 (SzczEPAŃSKI 1969). If the
self demand of energy consumed by roots and rhizomes is such as for the
aerial shoots, then the photosynthetical apparatus must produce 4 times more
of organic matter than estimated maximal biomass of aerial parts.

Assuming all this the gross production of reeds of Mikołajskie Lake would
be 25 t/ha organic matter, or 27 t/ha dry weight. Only then this value can be
compared with the plankton production. The primary net production of aerial
parts of reeds is 6.2 t organic matter/ha/year (KOWALCZEWSKI and WASILEWSKI
1966). The vegetation period for reed till its maximal biomass is about 150
days, and assuming that the production is equal during all this period, the
values of 16.7 g organic matter/m²/day are obtained. Thus the gross primary
production of a reed bed, without taking into consideration the littoral plan-
kton and periphyton production, is about ten times higher than the gross
production of pelagial (2.40 g O_2/m²/day — SzczEPAŃSKI 1966), 5.5 g O_2/m²/
/day — WINBERG 1960). From this amount, however, only 6.2 t organic mat-
ter/ha, i.e. an aerial parts biomass can be available for consumers in the
lake. This production is not high.

LIETH (1965) quotes the maximal production values for various latitudes.
The table below is taken from his paper:

Latitude N or S	10-20	20-30	30-40	40-50	50-60	60-70	70-80
Production dry weight t/ha/year	75	54	37	33	27	4-6	1-4

The decomposition of submerged macrophytes is very rapid due to the
participation of various consumers. The emergent macrophytes are not so
popular. I am not taking into consideration species which are specialized pa-
rasites of macrophytes, e.g. aphids, as they lower the production, but do not
decompose the macrophyte tissues. A dead reed can be deposited in water for
a very long time without changing its morphological character (three years
of observations). From such a material, after depositing in water, the mineral
salts are washed out very rapidly (P and K 15–30 min — materials of PLANTER,
presented on the Meeting in Świnoujście). The organic parts, however, are
strongly resistant to decomposition. They lose their mechanical endurance, the
wave action changes it into detritus, which is taken by consumers in this
form, or transported to pelagial where it forms sediment. It is possible that
several passages through the alimentary canals of consumers increases the
assimilation of this kind of primary production. Very often, however, unused
remains of macrophytes are deposited in sediments forming peat of peat bogs.

Taking the above into consideration, the investigations of primary produc-
tion should be treated as one of the aspects of bioenergetics of water reser-
voirs, and when considering the availability and assimilation of the produced
plant matter, and the properly estimated calorific value, it is possible to esti-
mate properly the primary production as a source of energy.

7*

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PRIMARY PRODUCTION OF PHYTOPLANKTON AND PRODUCTION OF CARPS IN PONDS

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ABSTRACT

The interrelations between phytoplankton primary production in ponds and carp production are discussed. A survey of methods of increasing the primary production up from the turn of 19th century and the modern methods are discussed, particularly the investigations carried out lately in the Laboratory of Water Biology, Polish Academy of Sciences.

Ponds, these artificial shallow water reservoirs, are foreseen for fish production, in our latitude — mainly for carp culture. Fish production in ponds is based on two alimentary sources — autochthonous and allochthonous. To the first source may be referred the secondary production of the lower aquatic animals, to the second one — the food produced outside and then supplied to the ponds.

Impossibility of separating the site, where natural food is produced, from the fish, forces to assign the present day system of fish culture in ponds to the highly primitive methods of animal production. Observing the existence of a relation between the individual trophic zones in water reservoirs we may suppose that the greater will be the fish production in ponds the higher will be the primary production. This relation has already been known long before, although the research methods applied at that time did not permit this relation to be determined more in detail. On the turn of the XIX century, just this relation was a basis for mineral fertilization of ponds.

The works made in 1914–1915 at Sachsenhausen, a locality so ingloriously distinguished later in the history, are today a classical example of an imperfection of the methods applied. Here in studies of mineral fertilization of ponds only qualitative and quantitative composition of phytoplankton has been taken into account (Pouly 1919). It appeared after a comparison of the results obtained during the research of both phytoplankton and fish productions that no relation existed between the phytoplankton and fish production there. The same results of studies on phytoplankton, calculated in the fifties by Winberg (1952) and presented in mass units, closely correlate with the increased fish production. Thus the presentation of the results of the studies on phytoplan-

kton in comparable units allowed the relation between these two trophic levels, fairly remote from each other, to be determined. It seems to be indisputable at present that exerting the influence on phytoplankton by adding mineral nutrients we may markedly increase fish production.

Fertilization of ponds by means of mineral substances appears today to be a drastic method, as concerns human interference in water environment. It leads to certain simplification of production process in ponds. The annual supply of nitrogen and phosphorus in mineral form makes that, in our climate, phytoplankton is the only product of organic substance in ponds, since vascular plants completely disappear, and periphyton does not play any important role.

It should be emphasized here that a more detailed determination of the relation between the phytoplankton and the increase in fish amounts in ponds was possible only due to the methods of measuring the primary production of phytoplankton. First calculations of the percentage of the energy accumulated in the fish bodies, in relation to the primary production, were made by WINBERG (1960), who obtained about 10.2%, together with the energy losses in metabolic processes, which make here about 2/3. Thus, the total amount of the energy accumulated in the fish bodies would be 3.4% of the primary production value. WINBERG declares, however, that in various ponds this percentage may markedly change. Similar calculations were made in the sixties by HEPHER (1962) for the ponds in Israel. The primary production in these ponds ranged, during a season, from 1.45 to 4.47 g C/m²/day (2.89 on the average). This, converted to energy units, amounts to 13.6–41.8 kcal/m²/day, i.e. 27 kcal/m²/day on the average. HEPHER, according to STRICKLAND (1960), has also reduced his results to the biomass of algae, and has referred the fish production to this biomass. The fish production at that time was 0.43 g/m²/day and made about 1.3–2.3% of the biomass. Expressing both the primary production and the fish increase in energy units we may state that the fish production was 1.6% of the primary production, thus being about 50% lower than that given by WINBERG.

In the Laboratory of Water Biology long-lasting measurements were conducted of the primary production of phytoplankton. The values of the phytoplankton production, given in Table I, are the average values of 10–15 measurements made during a season (WRÓBEL 1962, 1965; FEREŃSKA and LEWKOWICZ 1966). In all the ponds here considered the same method was always used in determining the primary production. This was the oxygen method of light and dark bottles, with the exposition time amounting to 24 hours. The measurements were made at two or three depth levels. This allowed the primary production cf phytoplankton to be calculated according to the areal units. Experimental farms, situated at Gołysz and Landek, where the research works were carried out, markedly differ in having various chemical composition of water. Calcium content in water of the Vistula River, which supplies the ponds at Gołysz, amounts to 22 mg/l on the average, whereas that of the Iłownica River, connected with the ponds at Landek, is twice as large. Additionally, the latter river is characterized by an increased content of magnesium that amounts here to 3 and 5 mg Mg/l (WRÓBEL 1965a). Due to the considerably greater amount of Ca in water of the ponds at Landek, the reaction of their bottom sediments is neutral, whereas in the Gołysz ponds this reaction ranges from 5 to 6 pH.

Table I. Primary production of phytoplankton and carp production in ponds

	Experi-mental farm	No. of pond	Year	Production of phytoplankton kcal/m²	Production of fish kcal/m²	Use of phytoplankton energy for fish production		Mortality
						net, %	gross, %	
Check ponds	Gołysz	6	1961	549	12.6	2.30	6.90	9.0
	,,	,,	1962	640	12.5	1.95	5.85	18.0
	,,	,,	1963	837	15.4	1.84	5.52	57.1
	,,	,,	1964	1128	16.5	1.46	4.38	41.0
	,,	ChM	1964	1000	17.3	1.73	5.19	1.5
	Landek	KM	1961	716	15.5	2.16	6.48	16.0
Fertilized ponds	Gołysz	2	1961	1705	42.6	2.50	7.50	10.0
	,,	3	1962	2774	51.5	1.86	5.58	5.0
	,,	,,	1963	2437	43.9	1.80	5.40	29.6
	,,	,,	1964	2035	44.8	2.20	6.60	50.6
	,,	4	1961	1774	51.3	2.89	8.67	12.0
	,,	,,	1962	1892	44.9	2.37	7.11	14.9
	,,	,,	1963	1657	25.0	1.51	4.53	17.0
	,,	5	1962	1713	32.5	1.90	5.70	46.4
	Landek	KS	1961	1293	35.7	2.76	8.28	43.0
	,,	KR	1961	2243	38.7	1.72	5.16	12.3

Note. Both phytoplankton production and fish production are given for a whole vegetative season, i.e. for 165 days.

The frequency of carps in the ponds considered was changing. So, in 1961 it was in the check ponds No. 6, ChM and KM about 300 per 1 ha. In the other ponds, in 1961, this was about 1300 per 1 ha, to reach even 2000 per 1 ha in the other years.

Except for check ponds, the remaining ponds were, during a season, several times (4–8 doses) fertilized with nitrogen and phosphorous substances. The total amount of the nitrogen did not exceed here 120 kg/ha, and that of the phosphorous substance — 22 kg/ha. The last column of Table I illustrates fish mortality in percentages. In various ponds and in various years this mortality ranged from 1.5 to 57%.

The above remarks are given to show various conditions of production (changing chemical composition of water) and various means of production intensification (fertilization, frequency of fish individuals).

During the calculation of fish production the calorific value of 1 kg carp was accepted to be equal to 1000 kcal.

Considering the oxygen method to be imperfect in estimating the primary production, particularly as concerns ponds characterized by a strong development of phytoplankton, and taking into account errors that result from the acceptance of the same calorific value for 1 kg fish, we should regard the calculation of the use of primary production by fish as approximate only. Apart from the diversity in conditions, a distinct relation has been noted to occur between the primary production of phytoplankton and fish production (correlation coefficient — $r = 0.89$). The average percentage of use of primary production of phytoplankton amounted to 2.06.

The influence of using the primary production upon the fish production in both check and fertilized ponds is also worthy of being stressed here. In the former ponds the use was lower and amounted to 1.84% on the average,

whereas in the latter ones it was 2.10%. Although the differences are not considerable here, distinct tendency may be observed, especially as concerns the greater effectiveness in the use of the primary production in the fertilized ponds. This may be explained by various composition of phytoplankton species in these two groups of ponds. In the ponds fertilized with the main phytoplankton components, representatives of the class Chlorophyceae, mainly Chlorococcales, were found during the whole season, whereas in the non-fertilized ponds, the species composition of plankton algae was considerably rich, characterized by the predominance of the species that belong to the groups Chrysophyceae and Conjugales (Bucka 1966).

When high frequency is noted (2000 individuals per 1 ha) the fish mortality does not greatly affect the use of the primary production. In 1962, the mortality in pond No. 6 reached 18%, and the degree of use was as much as 1.95%. In the next year, it decreased to 1.84% only, and the mortality was 57.1%. In the KS pond the degree of use of the primary production of phytoplankton was in 1961 even greater than in the pond KR, irrespective of the fact that fish mortality in the first pond was 3.5 times greater. In both ponds the mass death of fish has not been observed, thus we may suppose that the high losses in carp individuals took place immediately after the stocking the ponds with fish.

The values of energy accumulation shown in the table are, in relation to the primary production of phytoplankton, additionally charged with another error that results in their decrease. Part of the organic substance produced in ponds is deposited on the bottom. The contents of organic substance in deposits and in water flowing away (Wróbel 1965) demonstrate that in the check pond about 24 g C/m^2 were accumulated and then lost with the outflow during the season of 165 days. In the fertilized pond, in turn, this was 48 g C/m^2, corresponding to 225 $kcal/m^2$ and 450 $kcal/m^2$. Approximately, this was 25% of the total primary production of these ponds. Thus, the above percentage relation between the fish production and primary production (2.06%) should be corrected by this value. In consequence of this, we may accept that the production of carps in the ponds here considered was 2.75% of the primary production of phytoplankton.

The data mentioned above do not pretend to be a detailed and universal estimation of the relation between the primary production of phytoplankton and fish production in ponds. They only present the production relations of the Experimental Farms of the Laboratory of Water Biology. These cannot even be compared with the other results obtained in Poland, since research in this field has merely been begun.

To the end of this paper, the values of energy accumulation in fish individuals, compared with the primary production, according to climatic zones, are also worthy of being repeated. The data obtained by Hepher (1.6%) are related to the ponds situated in the area of the 27 parallel of N latitude, whereas those presented in this article (2.75%) concern the ponds found to occur at the 50 parallel, and those discussed by Winberg (3.4%) — are obtained in the ponds situated even beyond the 54 parallel. Thus, it may be seen that with the decrease in temperature the fish production is distinctly affected by the use of primary production.

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PRODUCTION OF CHEMOSYNTHETIZING BACTERIA AS A CHAIN OF ENERGY RECUPERATION BY AQUATIC BIOCENOSIS

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ABSTRACT

The energy flow through the ecosystem of a water body is discussed with regard to the energy recuperation from chemical compounds derived from the destruction of organic substance. The amount of energy accumulated by chemosynthetizing bacteria is compared with the photosynthetic algal production in the experimental water body. The range of values was similar. The phytoplankton production was greater than the production of chemosynthetizing bacteria only in summer. In the other seasons of the year the production of chemosynthetizing bacteria was considerably greater.

Production of chemosynthetizing microorganisms as opposed to production of photosynthetizing organisms is characterized by the fact that not solar energy but energy drawn from oxidation of simple chemical substances is the source of energy indispensable for their vital processes. Despite this difference, in both these cases an organic substance is produced out of inorganic compounds. Attention should be paid to the fact that in the diagram of energy flow the chain of chemical synthesis is differently situated than the chain of photosynthesis (Fig. 1).

Some authors are of opinion that the origins of life should be looked for in processes of chemosynthesis, and therefore bacterial chemosynthesis could be treated as primary production. We have to agree, that chemical substances formed as a result of destruction of remains of dead organisms, which were formed by means of photosynthesis, and by destruction of the consumers of these organisms, are used in our geological era as an energy source for chemosynthesis processes. In this case the process of chemosynthesis is not a process of primary production, but a process of energy recuperation. Destruction process is also to some extent a process of energy recuperation as some of the energy contained in the dead matter pass to the cells of heterotrophic bacteria, energy of which returns to a higher trophic level. However, this process is not discussed as it does not belong to the subject of this paper.

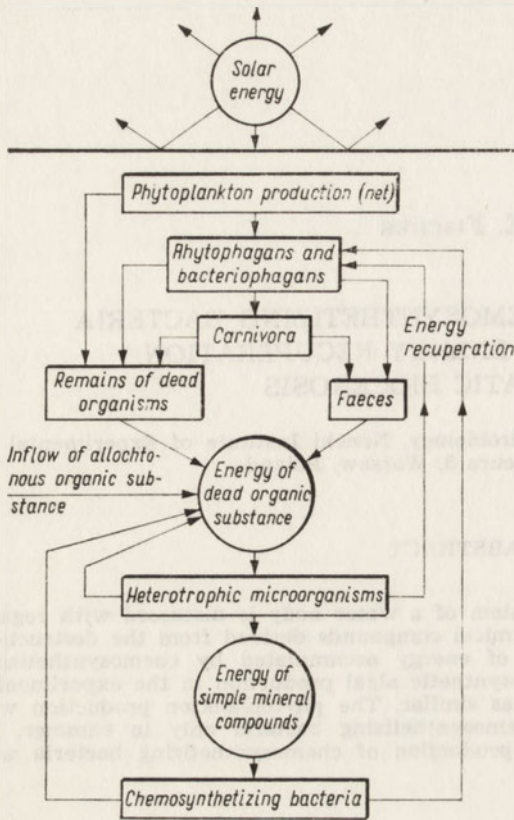The problem of consequence and significance of the chemosynthesis process

Fig. 1. Simplified diagram of net energy flow in various trophic levels of the water body

in the water body is not sufficiently tested yet and requires further investigations.

Chemical composition of bacteria (also chemosynthetizing) is similar to the chemical composition of plant tissue and brawns of fish and ruminants (Anderson 1948, Starmach 1963, Rodina 1958) (Table I). Thus the nutritious value of chemosynthetizing microorganisms is not worse than that of phytoplankton. Therefore their significance for the biocenosis of water body should be ex-

Table I. Chemical composition of various organisms

Object	Contents in %				Authors
	proteins	carbo-hydrates	lipides	ashes	
Bacteria	12.5–87.5	12.0–28.0	1.0–41.0	2.0–30.0	Anderson 1948
Blue-green algae	to 35	to 75	to 10	10–20	Starmach 1963
Brawns of fish	48.0–85.1	—	0.1–54.0	0.5–5.6	Rodina 1958
Brawns of ruminants	87	2	7	4	

amined from the quantitative standpoint. A question arises, whether production of so small microorganisms may be comparable with phytoplankton production.

The difference between the static trophic pyramid and the dynamic process of energy flow through the biocenosis of the water body should be remembered. The biomass of chemosynthetizing bacteria is minute; in one litre of bottom sediment, where the density of bacteria is the greatest as compared with the rest of the water body (up to 10^{11} cells/1 l of sediment), their dry weight is low — the utmost 1 mg/l. But their production depends (as it has been proved during our investigations) not as much on the current state of bacteria biomass as on the conditions guiding their development and it may be high (e.g. in case of our investigations up to 70 mg/l/24hr).

Despite the opinions of some authors, the complete futility of bioenergy investigations should be pointed out, as they determine the standing crop of bacterial population by the counting of cells without designating simultaneously in detail the dimension of this population. The range of these dimensions may be quite big.

As an example may be used here investigations of the bacteria population composition of one of the experimental culture ponds at the Department of Fish Culture, Institute of Inland Fisheries in Żabieniec. The investigations were carried out using the method of microphotography (Fig. 2).

As it can be seen the cells were very differentiated as to their dimension. The main difficulty of estimating the value of bacterial biomass by counting the cells is the precise measurement of these cells. E.g., an error of 0.2 μ in estimating the diameter of globular cells of a real diameter 1 μ results in an error of some 50% in estimating its volume.

An answer to the question about the quantitative significance of the chemosynthesis process in energetic processes of the water body, and to what extent this production may be compared with phytoplankton production, may be expected to be given by comparative studies of microphytoplankton production and production of chemosynthetizing bacteria. This same method of measurement should be used for both groups of organisms.

The common feature for those two groups of organisms is drawing carbon for constructing cells from the same source i.e. CO_2. Therefore in our investigations the carbon sampled by these organisms during the production process was labelled with the method of ^{14}C-labelled. Out of the amount of sampled carbon it is easy to estimate the amount of produced biomass in units of dry weight, using the already known in literature indicators of carbon contents in phytoplankton and chemosynthetizing bacteria. On the authority of the investigations of different authors, quoted in literature, and dealing with the chemical composition of bacteria and algae, attempts were made at comparative determining the calorific value of biomasses of chemosynthetizing bacteria and microphytoplankton produced in the experimental water body. It is generally accepted that the energetic significance of phytoplankton biomass is uncomparably greater than that of the biomass produced by means of energy recuperation due to chemosynthetizing bacteria. Therefore values were compared assuming the optimum conditions to determine the values of photosynthesis products as opposed to estimations of the values of chemosynthesis products. Therefore the volume of phytoplankton production during 24hr in water layer under the surface of 1 square metre was assumed as a basis taking

Fig. 2. Exemplary photograph of the section of Coli-5 membrane filter with bacterial sediment from a sample of pond water

into consideration the thickness of water layer on the day of investigations. The biomass production of chemosynthetizing bacteria was estimated out of 1 square metre but only in a sediment layer 3 cm thick. Apart from that, for calculations, one of the greatest calorific values of algae was chosen i.e. the one determined by STARMACH (1963) as 4.41 kcal/g of blue-green algae dry weight. On the other hand, for bacteria — according to the chemical composition of bacteria determined by ANDERSON (1948) — within the limits of the lowest calorific values of bacteria dry weight (4.3 kcal/g).

The results of weekly measurements show that the biomass produced during 24hr by means of chemosynthesis gives in some seasons of the year values comparable with the values of microphytoplankton production. In other seasons of the year it is lower or many times higher than the values of phytoplankton production.

Figure 3 shows that the greatest amounts of carbon assimilated in the 24hr production process of bacterial mass take place in the summer period — up to 1.15 g C/m²/24hr. In spring, the amount is relatively big, within the limits of 0.4 g C/m²/24hr. But in winter and autumn the amount is on a relatively even level, on the average about 0.04 g C/m²/24hr.

Microphytoplankton production during 24hr in days of sampling, is also the
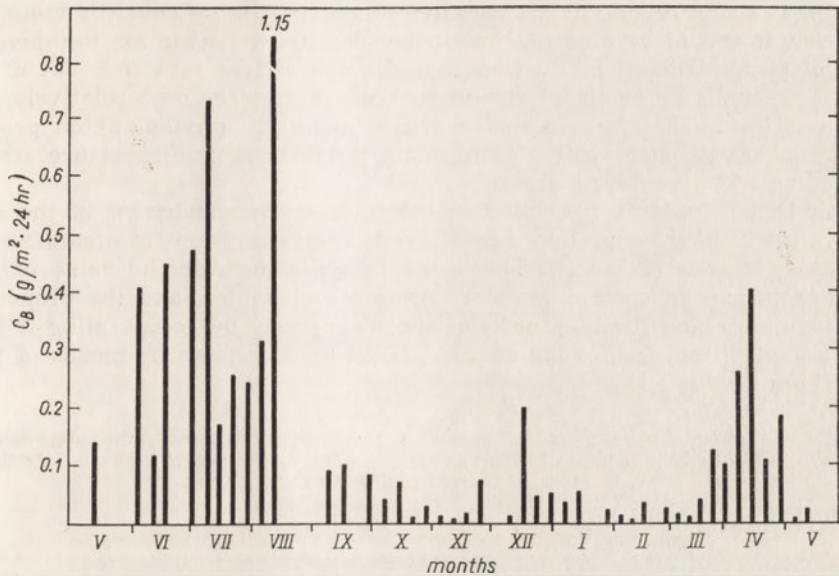
Fig. 3. Production of chemosynthetizing bacteria expressed in quantities of carbon assimilated during 24hr
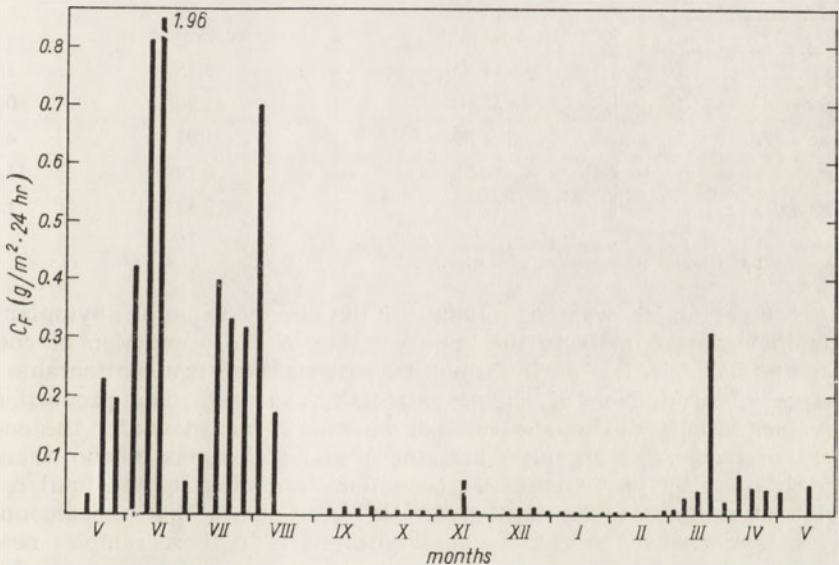

Fig. 4. Microphytoplankton production in the amount of assimilated carbon during 24hr

greatest in summer (Fig. 4), which could be expected on account of the insolation of the water body. The spring period has definitely lower values. In autumn, photosynthesis reaches even lower values, and it is almost 0 in winter.

Undoubtedly, the production deriving its energy from sunlight during

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autumn, at a short sunny day, and in winter, under the ice cover, is minimum. However, it should be noticed, that in periods unfavourable for the development of phytoplankton production reproduction of live substance out of mineral compounds by means of chemosynthesis takes place on a relatively high and even level. Therefore in the period of decreased phytoplankton production by means of photosynthesis, the main producer of live substance are the proceeding recuperation processes.

This is more vividly presented in the table with comparisons of the calorific values of biomass produced by the two analysed groups of organisms, for respective seasons (Table II). The Table presents the calorific value of produced biomasses in spring, summer, autumn and winter, and the proportion of energy enriching the biocenosis of the water body by recuperating it from dead organism remains, to the energy gained by biocenosis by means of phytoplankton production.

Table II. Comparison of seasonal production of chemosynthetizing and photosynthetizing organisms in relation to 1 m² of the surface of experimental water body. Water-level 6–34 cm, investigated layer of bottom sediment: 3 cm

Season	Number of 24hr experiments	Production of chemosynthetizing microorganisms for the experiment	Production of photosynthetizing microplankton for the experiment	$\dfrac{P_B}{P_F}$
	n	P_B	P_F	
		kcal/m²*	kcal/m²**	
Spring	10	9.42	5.35	1.76
Summer	10	36.80	43.36	0.85
Autumn	11	4.43	1.07	4.14
Winter	11	4.22	0.28	15.07
On average		13.72	12.52	1.10

* Assumed: 4.3 kcal of dry weight with ashes.
** Assumed: 4.41 kcal/g of dry weight with ashes.

This comparison shows, that in summer the energy value of phytoplankton production is approximate to the energy value of the production of chemosynthetizing bacteria. But during the other seasons there is a considerable predominance of production of chemosynthetizing bacteria. The proportion of these values is only during the summer near to 1, but in winter the energy recuperated from dead organism remains is about 15 times greater than the energy obtained by phytoplankton production. Summing up the total calorific value of samples taken throughout the year shows that the amount of energy recuperated by means of chemosynthesis is in these samples near to the sum of calorific value of microphytoplankton produced by means of photosynthesis.

As the changes of such factors e.g. temperature, changes of chemical factors in the habitat, which rule the production of chemosynthetizing bacteria, do not undergo such rapid fluctuations as light, it was possible (as opposed to photosynthesis) to calculate approximately the energy flow to other trophic levels of the water body by means of recuperation in the annual summing up (Table III). During the period of investigations, which lasted 354 days, the

Table III. Production of chemosynthetizing bacteria in respective seasons of the year, in relation to 1 m² of the surface of experimental water body. Water-level 6–34 cm, investigated layer of bottom sediment: 3 cm

Season	Number of days during the season	Twenty-four hours' average production during the season (kcal/m²/24hr)	Total production during the season (kcal/m²)
Spring	80	0.942	75.36
Summer	92	3.680	338.56
Autumn	92	0.402	37.39
Winter	90	0.384	34.56
Total	354	—	485.87

biocenosis of the investigated water body by means of recuperation by chemosynthesis gained altogether 485.87 kcal/m²/hr.

To end with, it should be emphasized that the estimation of the significance of energy recuperation in chemosynthesis processes cannot be generalized for all water bodies. Still its significance has not yet been investigated in deep water bodies, where the light does not reach the deeper layers. Investigations of the Rybinski dam reservoir carried out by Kuznetzov et al. (1966) showed that the carbon assimilation calculated only in the vegetational period for phytoplankton and bacteria under the surface of 1 square metre is comparable, and these values trend in approximate limits. However, it seems that the production of chemosynthetizing organisms, and especially of shallow water bodies and littoral of great water bodies, is worth paying so much attention in investigations.

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8*

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GENERATION TIME OF A GROUP OF BACTERIA IN THE WATER OF MAZURIAN LAKES

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ABSTRACT

The results of investigations on the generation time of a group of bacteria in the water of 7 Mazurian Lakes are presented. The counted generation time was greatly differentiated (2.9–70.0 hr) in the initial and following stages of bacterial growth, depending on the time of exposure.

Slight differentiations (2.9–6.5 hr) took place in the logarithmic phase, which in the examined groups occurred between the 2nd and 8th hour of incubation, depending on the trophic type of the examined lake.

The results that have been already obtained (Gcdlewska-Lifowa 1969) showed the necessity to apply a determined and rather brief exposure time, while estimating the generation time of a group of bacteria in water.

This work aimed at an analysis of the dependence between the length of generation time of a group of bacteria in water and the time of exposure of several Mazurian Lakes of different trophic type, with the help of Razumov's method (Razumov 1948).

Total number of bacteria before and after incubation was counted on membrane filters Coli-5 — Sartorius coloured with 5% erythrosine in 5% phenolated water.

In all experiments the water was taken from the surface layer of epilimnion (0.1–0.2 m). Zooplankton was removed out of water by means of filtering through cotton wool.

On the basis of the experiments that have been carried out, it can be said, that the intensive increase in number of bacteria took place during the first hours of exposure. The longer was the time of incubation the number of bacterial cells gradually decreased. Out of the obtained total number of bacteria, the generation time of a group of bacteria in water was calculated according to the Razumov's formula. The calculated generation time for different lakes considerably differs depending on the exposure and the growth phase of a group of bacteria.

For Lake Mamry these values were 70hr after one hour of incubation, 6.1 after 5hr of incubation, and 69 after 24hr (Fig. 1A, 1B).

For the other lakes these values also underwent some changes, which depended on how long the experiment lasted.
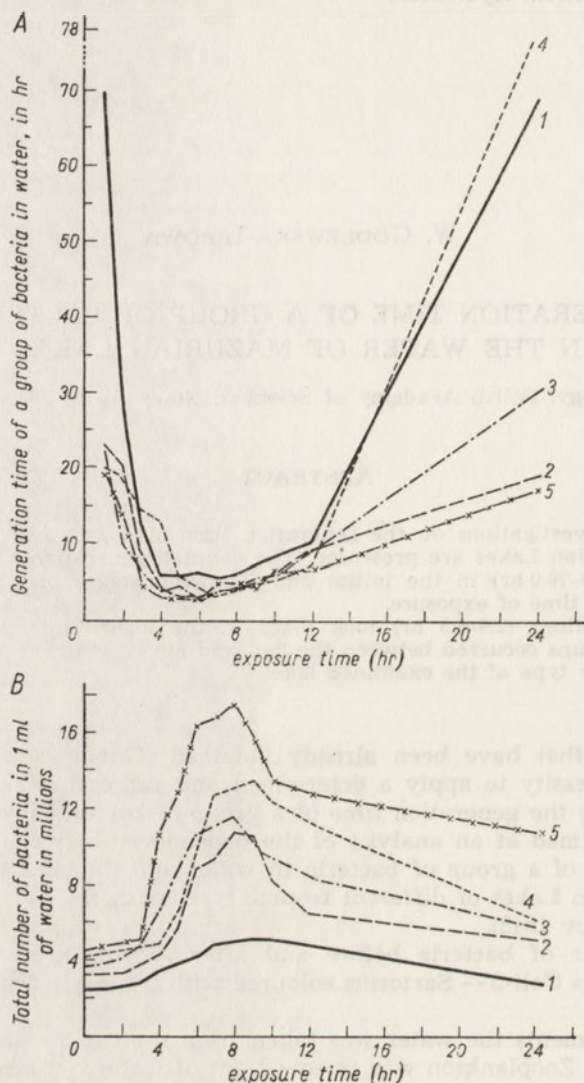
Fig. 1. A — Generation time of a group of bacteria in water, in 5 Mazurian Lakes.
1 — Mamry (oligotroph.), 2 — Tałtowisko (mesotroph.), 3 — Mikołajskie (eutroph.),
4 — Sniardwy (eutroph.), 5 — Bełdany (high degree of eutrophy). B — Number dy-
namics of a group of bacteria in the water of 5 Mazurian Lakes. 1 — Mamry (oli-
gotroph.), 2 — Tałtowisko (mesotroph.), 3 — Mikołajskie (eutroph.), 4 — Sniardwy
(eutroph.), 5 — Bełdany (high degree eutrophy)

Great differences in the generation time were observed in the investigated
lakes in the initial and final phases of bacterial growth, while in the logarith-
mic phase these differences, and especially in eutrophic lakes, were very
slight.

The lakes having the lowest trophy displayed slightly longer generation
time than eutrophic lakes, and the lakes polluted with industrial sewage wa-
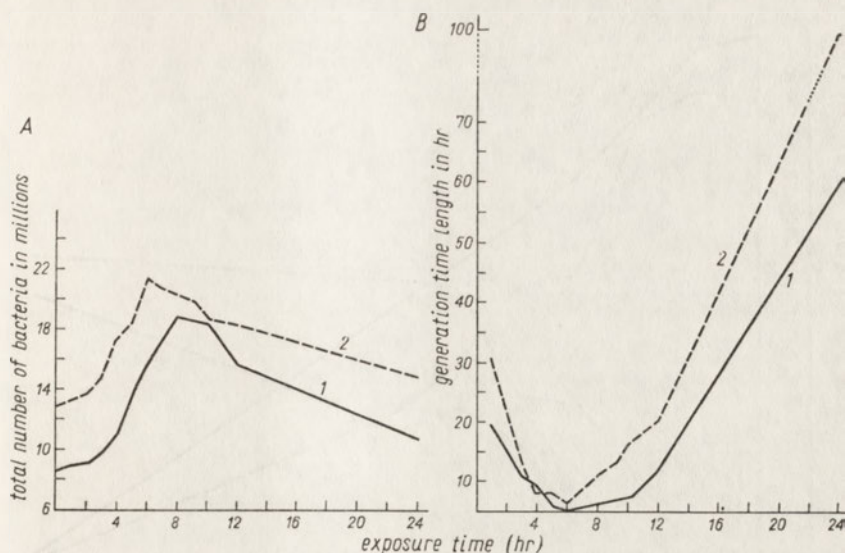ters slightly longer than the latter (lakes Nidzkie and Guzianka) (Fig. 2A, 2B).

Fig. 2. A — total number of bacteria in 1 ml water in millions. 1 — Lake Nidzkie, 2 — Lake Guzianka. B — generation time of a group of bacteria in water. 1 — Lake Nidzkie, 2 — Lake Guzianka
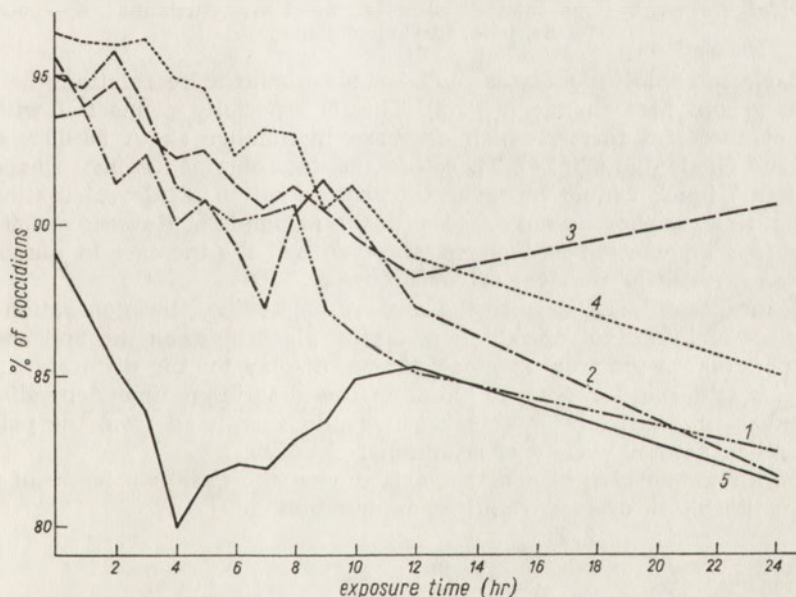

Fig. 3. Changes of the percentage participation of coccoidal forms, in the total number of bacteria, after different time of exposure, in 5 Mazurian Lakes. 1 — Sniardwy, 2 — Mikolajskie, 3 — Tałtowisko, 4 — Mamry, 5 — Bełdany

Analysing the respective morphological forms of bacteria found in the investigated lakes, it can be said, that already after 8–10hr not only the num-
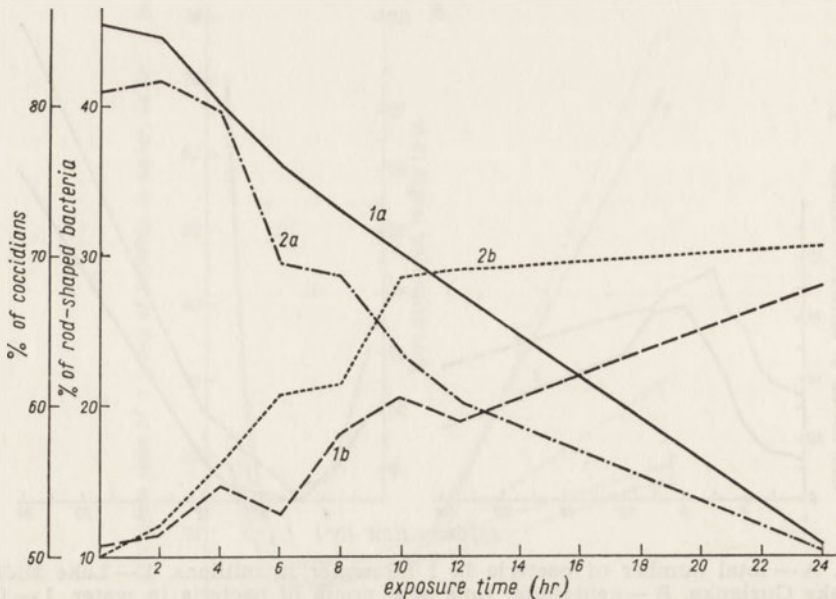
Fig. 4. Changes in the percentage of rod-shaped bacteria and coccoidal forms in the total number of bacteria, after different time of exposure. 1 — Lake Nidzkie: a — coccoidal forms, b — rod-shaped bacteria. 2 — Lake Guzianka: a — coccoidal forms, b — rod-shaped bacteria

ber of bacteria rapidly decreases but also the quantitative relations between dominant groups also change (Fig. 3). This is especially connected with the number of coccoidal forms, which decrease in number about 50–60% (Lake Nidzkie and Guzianka) (Fig. 4). Therefore the data obtained from an exposure longer than 7 hours cannot be taken into consideration, while calculating the generation time, as they do not agree with the principle of RAZUMOV's method, which as it is known, is based on measurements of the increase in number of bacteria as a result of removal of consumers.

In all discussed lakes, despite the variety of medium, the generation time in the phase of intensive reproduction, taking place between the 2nd and 8th hour (depending on the trophic type), did not display too big differences.

There is still the necessity to examine the generation time depending on the exposure time on some more lakes more differentiated from the point of trophy and in greater variety of situations.

Also the slow development of bacteria during the first two hours of incubation, in the phase of lags, requires explanation.

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WATER ORGANIC MATTER RESSOURCES
OF HIGH DISPERSION

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ABSTRACT

A survey of data is given on water organic matter and its ecological role in an
aquatic ecosystem, with particular stress on its stability and its possible place in
food chains including heterotrophic microorganisms.

This paper aims at presenting a survey of data, chiefly published ones,
concerning organic matter dispersed in natural waters. To delimit the degree
of dispersion one should remind that particles passing through membrane fil-
ters of pore diameter below 0.5 micron are usually assumed as soluble (col-
loidal and molecular), larger ones being reckoned with particulate matter
(Olson and Olsen 1967, Strickland 1965). The exploration of organic sub-
stances, particularly those highly dispersed, occurring in natural surface wa-
ters, undergoes a characteristic evolution. One of the first steps of investiga-
tion of water organic matter was elemental analysis and search for analogies
with the composition of animal and plant organisms (Birge and Juday 1934
after Skopintzev 1950). A further step was the identification of particular
groups of organic compounds like proteins, amino acids, carbohydrates, orga-
nic acids and other, occurring in both water and bottom sediments (Vallen-
tyne 1957). Recently more attention is given to a possible ecological role of
these substances in water. This role remains still poorly known in view of
diversity of these substances and of conditions in which they might manifest
their action. As example may serve substances controlling the number of
specimens in dense animal populations or substances acting selectively in in-
terspecific or interspecific relations, like inhibitors or stimulators of growth,
attractants, repellents, toxins and other (Styczyńska-Jurewicz 1967). For
example Fogg and Westlake (1955) have pointed to the role played by poly-
peptides excreted by live cells of various algae in neutralizing the harmful
effect of copper ions in water and at the same time in raising the assimila-
bility of iron. The vitamins and some other products excreted by aquatic
organisms were found to be decisive factors in mutual relationships within the
aquatic biocenoses (Droop 1968, Gold 1967, Kalle 1968, Lund 1965, Pourriot
1966, Watt 1966). Extracellular enzymes seem to enable some aquatic micro-

organisms to utilize dissolved organic compounds (Khailov and Gorbenko 1967, Overbeck 1961, Reichardt et al. 1967). After Shapiro (1957) the effect on aquatic environment of the refractory organic fraction is very fine and reveals oneself only in prolonged action. Evidence is supplied that this action is beneficial towards growth of phytoplankton (Prakash and Rashid 1968, Wetzel 1968). This subject requires obviously further investigation.

The non-specific role of water organic matter as a link in food chains seems to be important primarily on account of rich ressources of this material in both inland and near-surface oceanic waters, containing as much as several grams of organic carbon per cubic metre (Table I). It is then of interest to

Table I. Unstable fractions of organic material in natural waters (exemplary values)

μg/l	Amino acid (protein)	Carbohydrate and acid	Lipid	Total cal/l
Lake				
Particulate	800	600	150	8
Dissolved	3000	5000	—	40
Sea				
Particulate	150	20	—	1
Dissolved	250	100	—	2

Lake: Kunicki-Goldfinger 1968, Semenov et al. 1968. Sea: Cowey 1963, Hobson 1967, Riley et al. 1965, Parsons and Strickland 1962.

examine the chemical composition of this material, its stability, that at the same time provides information on its origin and its assimilability to consumers and finally its ability of being transformed into suspension of fine solid particles — of nannoseston — suitable for zooplankton filter feeding.

One should emphasize that the question is here of standing crop of organic matter, not of its production, nevertheless these values are approximate if yearly production per unit of volume of water column is considered (Khailov 1968). The ratio of particulate to dissolved material is usually very low, the dissolved one constituting chiefly the refractory — so called — humic fraction, exceeding several times the more easily decomposable fractions represented in Table I (Armstrong and Tibbits 1968, Forsberg 1967, Menzel 1967, Menzel and Ryther 1964, Newell and Kerr 1968, Ryhänen 1968, Skopintzev and Bakulina 1966, Williams 1967). The suspended particles are formed mainly from dead cell material, however attempts were made to distinguish within them the live bacterial cells fraction (Daumas and Fiala 1969, Holm-Hansen et al. 1968, Krey 1964).

The nutrient value of organic substances of the nannoseston was the object of numerous experiments, especially as regards the feeding of filtrators (Błażka 1966, 1967; Hillbricht-Ilkowska et al. 1966, Monakov and Sorokin 1960, Otsuki et al. 1969, Schmidt 1968). These papers point out some algal species as best food for the examined Daphnia sp., on the other hand they demonstrate that Daphnia grow also well when fed with detritus, bacterioplankton or with cultures of bacteria, protozoa and yeasts. This fact is of importance in periods of low photosynthesis when heterotrophic microorganisms may form a substitutional food base. According to Jannasch (1964) and

Scrokin (1965) numerous proofs exist that bacteria, beside their role of reducers mineralizing organic substances, store a considerable part of energy of these substances in their biomass, making available to secondary trophic levels the energy, which is inaccessible for them on another way. Both processes are involved here, that of chemoauthotrophy, discussed in details by E. Fischer (1970), and that of heterotrophy with utilization of refractory material, e.g. the allochtonic one of soil origin (Kuznetzov et al. 1967, Ryhänen 1968).

On the other hand the dependence of saprophytic bacteria on algal primary production is particularly manifest from the succession of abundant growth of these two groups (Duursma 1965, Golterman 1968, Overbeck 1968, Overbeck and Babenzien 1964, Walsh 1966). This might corroborate the opinion represented by many authors, that heterotrophic microorganisms are an indispensable link for utilization of dissolved substances by zooplankton (ZoBell 1946).

The heterotrophic process seems then to be the most important one in which a part of dissolved organic substances may be converted into a form accessible to zooplankton, saving at the same time its energetic level, although other ways exist of transforming dissolved matter into particulate one (see below).

If nannoseston is considered, a fraction of bottom sediments may be also taken into account, that in favourable conditions passes again into suspended form (Rybak 1970) the particle dimensions of which fitting into food requirements of particular animal groups (Gliwicz 1967). Seston particles that formed once a part of bottom sediments would constitute a material biologically more resistant to decomposition than, for example, fragments of algal cells short after their death; on the other hand organic constituents of seston neither are of identical age, except for mass appearance followed by dying of organisms of a single species.

A similar situation occurs with dissolved substances, because of the coexistence of compounds as easily assimilable as sugars, amino acids or organic phosphates, together with compounds as stable as humolimnic acid, isolated from lake water by Shapiro (1957) and Fluoreszenzstoff or Gelbstoff — brown coloured material isolated from sea water by Kalle (1962), and a series of compounds of intermediary character. In extreme conditions of decomposition of large masses of plant material in water a marked predominance of a certain group of compounds occurs, followed by an aperiodical set of transformations in the course of which a major part of the material undergoes mineralization (Dowgiałło 1966, Golterman 1964, Gorbunov 1962, Krause 1964, Solski 1962). At the same time a stabilized organic material is formed, rich in relatively refractory fraction, that still undergoes further mineralization, though considerably slower. This material as a whole still exhibits chemical properties of definite groups, like proteins, or carbohydrates, but contains also a phenolic (aromatic) component and may be rich in mineral fraction (Blażka 1966, Maciolek 1962, Semenov et al. 1968, Shapiro 1957). The energetic value of this material remains high; using the oxycalorie coefficient 3.4 kcal per 1 gram oxygen consumed in chemical oxidation (Maciolek 1962) a calorific value of about 4.5 kcal/g is obtained. The discussed material contains a few per cent of nitrogen in the form of organic compounds, chiefly amino nitrogen, the authochthonic — typically aquatic organic matter, particularly marine, being more abounding in nitrogen (Armstrong and Tibbits 1968, Cowey 1963, Par-

Table II. Water organic matter and organic nitrogen: nannoseston and dissolved. Comparison of Values: lowest —1; most frequent — 2;

Water body	Oxygen consumed (bichromate) mgO_2/l, water			Organic carbon[a] mgC/l, water			Organic matter[b] cal/l, water		
	1	2	3	1	2	3	1	2	3
Dam reservoir Zegrzyński	10	25	70	4	9	26	34	85	240
Astatic pool Przyjemny	45	90	150	16	34	56	150	300	500
Astatic pool Tundrowy	50	100	230	18	37	86	170	330	780
Astatic pool Przy szlaku	50	60	100	18	22	37	170	200	340
Astatic pools average	50	80	160	17	31	60	165	280	540

Water: filtered trough plankton net of 100–120 pore diameter. Nannoseston: obtained from filtred water by con-
[c] From analysis for protein, lipid and carbohydrate (Błażka 1966a). [d] mgN/l $\times 6.25 \times 4.6$.

SONS and STRICKLAND 1962, RILEY et al. 1965) than that from inland waters, supplied by drainage from surrounding soils (FORSBERG 1967, MACIOLEK 1962, RYHÄNEN 1968, SEMENOV et al. 1968) (Table II).

The stability of organic material estimated for oceanic water samples comes up to 1–2 years (KHAILOV 1968). In experiments, where oxygen consumption for biological mineralization of this material was determined, it was incomplete even after two years (RILEY et al. 1965). For the sake of comparison, stabilized soil humus is considered to reach the age of 50–800 years on the basis of the ratio of carbon isotopes (MORTENSEN and HIMES 1964, MATHUR and PAUL 1966). The less stable part of the latter material, characterized by lower molecular weight and higher solubility in water, attains the water bodies.

Beside the solubility the main difference between soil and water organic matter consists probably in its origin. Taking no account of different views on whether the formation of stable humus fraction results from enzymatic condensation or abiotic synthesis, one should remind that differences between authochthonic water humus and the allochthonic one result from the different initial material (e.g. algae producing no true lignin and vascular plants containing it in large proportion), and from different conditions of synthesis (lower substrate concentrations and lower degree of polymerization of the final product in water in comparison with soil conditions).

Another difference is that proteinaceous material participates to a high degree in the formation of aquatic humus, whereas the fraction most easily leached from soils contains not much organic nitrogen (DUURSMA 1967, KALLE 1962, LEONOWICZ and TROJANOWSKI 1967, TROJANOWSKI 1961, SIEBURTH and JENSEN 1969).

An inference seems to be justified here that the assimilability of a given organic substance for a consumer (with no account of the kind of consumer) should be inversely proportional to the time that elapsed since this substance belonged to a live cell. This seems however true only when a material without

a dam reservoir and astatic pools (unpublished data of Kędzierski, 1965–1967).
highest —3

Organic matter[c] cal/l, nannoseston			Organic nitrogen mg N/l; water,			Organic nitrogen mg N/l, nannoseston			Protein[d] cal/l, nannoseston		
1	2	3	1	2	3	1	2	3	1	2	3
6	10	20	0.7	1	1.6	0.1	0.25	0.4	3	7	11
3.5	20	92	1.3	2	4.5	0.1	0.3	1.8	3	8	52
4	10	134	1.5	3	9	0.1	0.2	2.7	3	6	78
2	3	14	1.1	1.2	2.6	0.03	0.05	0.35	0.8	1.5	10
3	11	80	1.3	2	5	0.1	0.2	1.6	2	5	46

tinuous centrifugation.　a Oxygen consumed $\times \frac{3}{8}$ (Skopintzev 1950).　b Oxygen consumed $\times 3.4$ (Maciolek 1962).

microorganisms is considered. Amorphous particles forming the surface layer of bottom sediments (Rodina 1963, Sebestyen 1964) as well as organic and even mineral particles suspended in the water column (Khailov and Finenko 1968, Kriss 1968) constitute an excellent substratum for numerous microorganisms which doubtless substantiate the value of this material as food for aquatic animals. Particles may act as surface for concentration of organic solutes by adsorption, or their material itself is utilized for building the microbial biomass, like polysaccharides of algal cell walls which resisted autholysis, animal and fungal chitin, glycoproteins and mucopolysaccharides chiefly of bacterial cell wall origin (Povoledo and Gerletti 1964, Mayaudon 1966). Even starch may occur abundantly in marine sediments in the form of free grains or undigested in the faeces of planktonic animals (Bursa 1968). Aquatic microorganisms, particularly marine, tend to stick together into bunches of several to thousands cells or to attach themselves to suspended solid particles, a small proportion of cells floating individually (Overbeck and Babenzien 1964, Rigomier 1967, Zobell 1967). This aggregation of microorganisms enables planktonic organisms to consume them together with other suspended particles.

The analogy of situation of organic solutes with that of suspended material as regards the change of their assimilability with time, is less clear than the analogy of chemical composition and calorific value, although the role of heterotrophic microorganisms seems even to be the more important here.

If then the fate of an insoluble cell fragment and the decrease with time of its content of substances assimilable to a filtering organism is considered, it is still the same fragment. At the same time the fate of carbon or nitrogen entering into the composition of soluble organic matter may be taken into account rather than that of the organic matter itself. The course of decomposition of lower sugars in soil is a good example of a history of an organic nutrient in natural environment. This was examined by adding to the soil glucose labelled with C^{14} and plants fed $C^{14}O_2$. Within few days more than the half

of carbon was mineralized to CO_2, the remaining one being incorporated into polysaccharides and proteins, which also succumbed mineralization, but much slower. Consequently, although no one of the soil organic compounds is imperishable, the polysaccharides retained the label as long as for several months and proteins even for several years. Presumably this is due in a certain degree to a state of dynamic equilibrium, where the same organic radical or CO_2 itself, containing radioactive carbon, is recycling many times, passing to microbial cells, often of different species, from the dying ones. The radioactive carbon is continuously excreted in the form of CO_2, however slowly enough to maintain its level in the polysaccharide or protein fraction practically constant for months or even years (CHESHIRE et al. 1968, HENNING 1967, KEEFER and MORTENSEN 1963, SIMONART 1964, SIMONART and MAYAUDON 1966).

It seems then more reasonable to discuss the fate of carbon of the soluble organic substances, of organic carbon, analogically to organic nitrogen or phosphorus, than the fate of individual substances.

As it was already mentioned, the water humus contains polysaccharide and protein fractions of a relatively high stability, similarly to soil humus. The sources of this stability may be various. The formation of organic-mineral complexes, as in soil, cannot be excluded, this factor however seems to be relevant rather as regards bottom sediments. Some elucidation of this problem may result from determination of ash content in the dispersed material, isolated from natural water e.g. by cryoconcentration (SHAPIRO 1961) followed by dialysis or fractionation on Sephadex. In the course of experiments on the decay of vascular plants in water, a high ash content was found (up to 30% of dry weight) in the amorphous suspension, accumulated owing to its high stability (DOWGIAŁŁO unpublished). This factor seems however to be rather less important with authochthonic material, except for the shore vegetation.

The stability of water organic matter may also originate in the process of enzymatic oxidation and condensation of aromatic units (e.g. aromatic amino acids) with proteins and polysaccharides from plants and microorganisms (KONONOVA 1958, TROJANCWSKI 1961). Even lower plants, like fungi, algae, lichens, that do not produce lignin, contain its aromatic precursors (DUURSMA 1967, SIEBURTH and JENSEN 1969).

The bacterial origin itself is insufficient as reason of stability of humic substances, although this view is still common in soil science. In soil the predominant conditions are those favourable to preservation of proteins and other substances owing to the formation of complexes of humic substances with protein, of lignoprotein, of minerals with protein, polysaccharide-mineral aggregates and many analogical systems. Lamellar structure of clay minerals favours adsorption and mechanical protection of high-molecular organic compounds from bacterial attack. MAYAUDON (1966) found that a labelled lipoproteinpolysaccharide from *Pseudomonas fluorescens* added to the soil was partially protected from bacterial decay due to the formation of a complex with humic acid. On the other hand a relatively high resistance of some bacterial or algal proteins against proteolytic enzymes cannot be excluded, as it is for example in the case of cyclic polypeptides (FOGG and WESTLAKE 1955).

It is then unlikely to indicate a natural organic substance resistant to adequately adapted microorganisms. After LISTON (1968) every organic particle entering the marine habitat is utilized by microorganisms settling in the shallow layer of bottom sediments, where the microbial process acts towards both

mineralization and conversion of organic matter into cellular material. This material is again accessible for organisms feeding on bacteria and unable to utilize refractory organic matter. The role of bacteria is relevant as regards the utilization of dissolved organic substances in concentration as low as a few micrograms per litre, contrary to algae, which are capable of heterotrophy only in concentration of two orders higher (ALLEN 1969, MUNRO and BROCK 1968, WRIGHT and HOBBIE 1966).

Another possible way exists, different from heterotrophy, of utilizing by filter-feeders of a part of dissolved substances. It has been found experimentally that air bubbles let through filtered sea water generate the formation of new aggregates, suitable for filtration, probably by coagulation of colloids. About 10 per cent of organic matter reserve of deep-sea water may be transformed on this way into suspended form in a quantity approximately equal to that of natural nannoseston and nearing it in chemical composition (BARBER 1966, JOHANNES 1967, MENZEL 1966, MENZEL and GOERING 1966, RILEY 1963, SHELDON et al. 1967). Also a part of dissolved material is transformed into filterable form by adsorption on suspended particles (KRISS 1968).

Contrary to these observations GERLETTI (1965) did not notice the formation of aggregates in lake water. On the other hand ŁAWACZ (1967) observed an increase of trypton sedimentation after a considerable cooling of lake water in autumn, at the same time the maximum concentration of soluble organic matter occurred. Yet the factor of strong water waving cannot be excluded here, analogically to the effect of shaking of net filtered lake water samples on the size increase of suspended particles (DOWGIAŁŁO unpublished). The marine particulate organic material obtained from the soluble one was assimilated by marine zooplankton, although to a lower extent than live phytoplankton. According to observations of BLAŻKA (1967) the humic material forms a reversible complex with protein which in the form of suspended particles may be ingested by *Daphnia* sp. when other source of food is lacking, its assimilability is however relatively low.

All this might corroborate the view that the role of heterotrophic microorganisms is relevant in transforming the soluble organic material into the food for zooplankton. The production of this material attains 5–10% of the primary production (DUURSMA 1965). The path of heterotrophy seems then to constitute a minor part of energetical transformations in an aquatic ecosystem, however the heterotrophic processes may supplement the food ressources in periods of its scarceness. Further investigations with the use of labelled organic material might throw some light 1) on the origin of the refractory fraction of soluble organic matter in natural waters, 2) on the extent to what it is utilized by heterotrophic microorganisms and directly by zooplankton.

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THE LEAF LITTER AS A FOOD SOURCE OF AQUATIC ORGANISMS IN THE RIVER THAMES***

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The significance of allochtonous matter in the form of tree leaves for the river ecosystem was investigated. The investigations were carried out on the River Thames near Reading, England. The amount of leaves falling into the river during the year was determined, and attempts were made to point out, which groups of organisms use these leaves as food. Therefore a field experiment was made. Oak, sycamore and willow leaves were placed on the bottom of the river, on a depth about 1.5 m, in nylon bags of two mesh size: coarse ones (3 mm) accessible to bottom fauna, and fine — (0.27 mm) not accessible for the majority of bottom fauna. Every month, bags with samples of leaves of a total initial dry weight 20 g were taken out of the river. When the deposited mineral material was rinsed on fine sieve then the fauna was taken out and counted. Then the dry weight of remaining leaves (dried at 65°C) was estimated, next milled, and afterwards the organic matter (by combustion at 650°C), calorific value (in bomb calorimeter) and nitrogen (by Kiejdahl's method) were determined.

The decrement rate of respective leaf species was the same in both types of bags, and so independent of the presence of fauna. Thus the fauna abundantly found in bags with coarse mesh, feeds with microorganisms and not with withering leaves. The disappearance of leaves is caused by microorganisms. Rich development of microorganisms was also explained by the observed increase of nitrogen in samples after two months of remaining in water. During the last two months of investigations the decrement rate was greater in bags with loose mesh and this was valid for all leaf species. In that period the leaves are already fragmented and are either carried by the river current or consumed by benthic animals.

The decomposition of willow leaves is the quickest, of oak leaves — the slowest, nevertheless the complete decomposition of the leaves of all species takes 1 year. Any substantial changes of the calorific value of organic matter

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were not observed, but the per cent of organic matter in dry weight of leaves underwent some fluctuations.

The total amount of leaves falling into Thames in the course of year is 1.59 kg of dry weight/m of bank line and 23.2 g of dry weight/m² of river surface.

The energy derived from leaves is an unsubstantial per cent of energy used by fish population in the river, while the leaves as a source of nitrogen seem to be of greater significance.

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ESTIMATION OF THE ENERGETIC VALUE OF NON-LIVING PARTICULATE ORGANIC MATTER (TRIPTON) BY TWO DIFFERENT METHODS

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ABSTRACT

On the example of tripton organic matter, it has been shown that the energy value determined by the chemical-calculative method considerably differs from the results obtained by direct combustion of samples in bomb calorimeter. This is probably the result of applying too high coefficients in the calculative method. Therefore independently of the accuracy of applied chemical methods, when analysing non--living organic matter, the calculative method to estimate the energy value of such material as tripton, seston, detritus or bottom sediments may be the reason of considerable errors.

Development of investigations on the productivity of ecosystems caused an increase of interest in energy value data of plant and animal organisms. Parallel to the constantly increasing information about the energy value of living organisms (GOLLEY 1959, CUMMINS 1967) a visible insufficiency of similar data is noticed in case of various forms of non-living organic matter in aquatic and terrestrial habitats: decayed plant and animal organisms in different decomposition stages, detritus, tripton, bottom sediments, organic substances dissolved in water. The opinions of some authors (ODUM and De la CRUZ 1963 or LUCAS 1958) about important role which play non-living organic matter in aquatic ecosystems, and also the possibility of transformation of dissolved organic substances into particles (SUTCLIFFE and BAYLOR 1963), which are accessible as food for animal organisms (JOHANNES 1967), point to the necessity of determining the energy value of these potential sources of food.

The work is an attempt to estimate the energy value of lake tripton (sedimentating non-living organic matter) in an annual cycle carried out at the same time by two different methods. Material for analyses was collected with the help of sedimentation traps (TUTIN 1955, OHLE 1964) placed on the depth of 10 m under the water surface (below epilimnion) and 1 m above the bottom (ŁAWACZ 1969). The exposure time of traps lasted two weeks. The collected tripton was dried in the temperature 105°C, then part of the material was combusted in the bomb calorimeter thus obtaining the energy value of dry tripton mass. The remaining material was used to determine the

amount of organic matter by burning in muffle furnace at a temperature 550°C, and to analyse the approximate composition of organic matter. The amount of fats was determined by weighing after 8-hour extraction with petroleum ether (Struszyński 1950). Protein was calculated by multiplying the amount of nitrogen — determined by Kjeldahl method — by the coefficient 6.25 (Birge and Juday 1926). When subtracting the sum of fats and protein from the total amount of organic matter the amount of carbohydrates was obtained. Multiplying the values obtained from analyses by energy
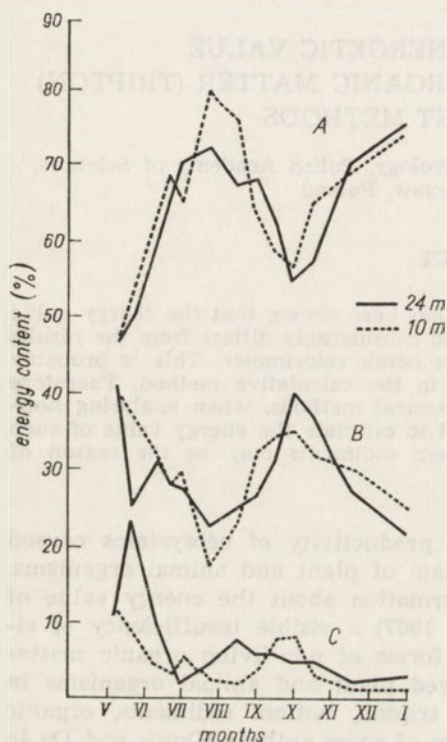
Fig. 1. Percentage participation of carbohydrates (A), proteins (B) and fats (C) in the total amount of energy (100%) in tripton organic matter

coefficients (fats — 9.4, protein — 5.7, carbohydrates — 4.5) the energy value of organic matter in the investigated sample was determined (Winberg et al. 1934).

The results obtained from an analysis of the composition of organic matter are presented on Fig. 1, where the participation of separate components (fats, proteins and carbohydrates) is expressed in per cents of energy derived from these compounds.

Fig. 2 presents a comparison of results obtained by the method of calculating the energy value basing on the qualitative composition of organic matter, with the energy value obtained by direct combustion of investigated sample in bomb calorimeter[1].

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[1] Eventual underestimation of calorific values by endothermic effect of bomb calorimeter (Paine 1966) is not important in the case of material to be analysed (relatively low calcium carbonate level).
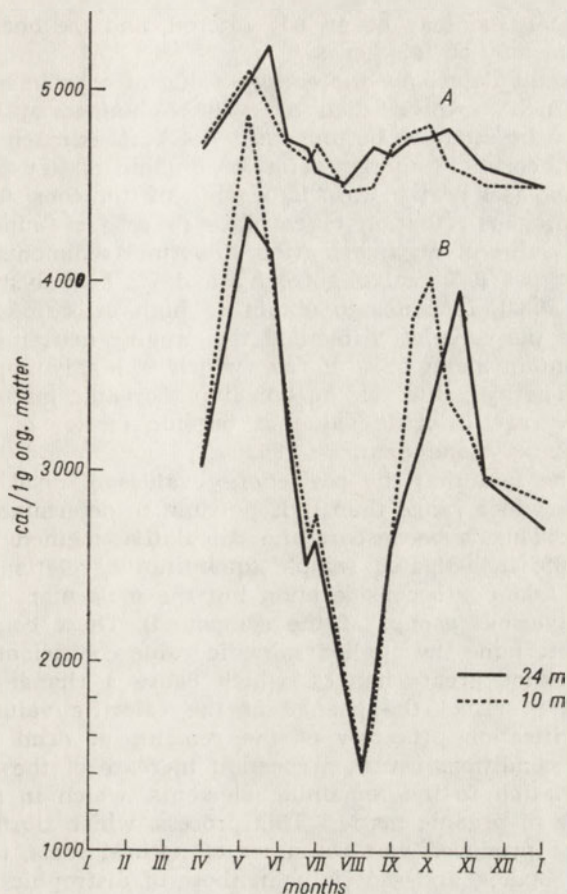
Fig. 2. Seasonal changes of the amount of energy contained by the organic matter of tripton and determined with the help of two methods. A — Calculative method, B — Combustion in bomb calorimeter

The results of these two methods differ considerably, where absolute values are concerned, but the course of the curves in the annual cycle displays a similar tendency. Definitely higher values obtained when using the calculative method (4.4–5.4 kcal per 1 g of organic matter) may be the result of the similar character of analytical methods, which render only the approximate composition of studied sample ("fats", "proteins" and "carbohydrates" applied in this method are not the exact equivalents of these compounds in the chemical sense). Also the method of calculating the amount of proteins by applying conversion coefficient (6.25) to nitrogen may be the source of error (VALLENTYNE 1957).

It seems, however, that the main reason of the existing divergence between the results of both methods are the too high (in this case) values of conversion coefficients applied for fats, proteins and carbohydrates. These compounds after the death of live organism undergo various decaying pro-

cesses in the water and may be greatly altered, and the energy coefficients accepted for them may be false ones.

These coefficients determine the energy value of organic matter to rather narrow limits, much narrower than the values obtained by the calorimeter method. As it can be seen the bottom limit (1.4 kcal) is much lower than the lowest possible theoretical energy value of organic matter when using the calculative method (4.3 kcal in case if organic matter consisted only of carbohydrates). Analogous situation takes place in case of minimum and maximum calorific value of organic matter of bottom sediments from lakes of various trophic types (0.7 kcal oligotrophy and 7.2 kcal dystrophy — RYBAK 1969, ALABYSEV 1932). In order to obtain so high calorific value (7.2 kcal) with the help of the calculative method the organic matter of bottom sediments should contain about 50% of fats, which is highly improbable. These sometimes high energy values of the non-living organic matter surpass considerably the average calorific value of organic matter of live organisms (5.6 kcal — OSTAPENIJA and SERGEEV 1963).

Thus it can be said that the real energy values of dead organic matter in nature have a wider range than it is possible to determine using the calculative method. This is because in the calculative method the elementary composition of the investigated sample (quantitative relations of respective elements) is not taken into consideration but the molecular composition (the quantity of the various groups of the compound). These compounds, which energy values determine the applied calorific value coefficients may undergo in natural conditions great changes, which cause a change of elementary composition and in effect the change of the calorific value. And so, for example, carbonification processes of the remains of dead animals taking place in natural conditions causes a constant increase of the amount of carbon atoms in relation to the remaining elements, which in result increases the energy value of organic matter. This process, which during the geological range of time produced vast resources of natural fuels, takes place also in several water bodies, and especially in those of distrophic type.

Contrary to this process, which can be included among reduction processes, is the oxidation phenomenon closely connected with the decrease of the calorific value of organic matter and smaller quantity of carbon in relation to other elements. Depending on several physico-chemical properties of aquatic habitat, among which the most important seem to be pH and the degree of oxygen saturation, the non-living organic matter becomes the subject of one of these processes.

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PERIPHYTON IN THE TROPHIC STRUCTURE
OF FRESHWATER ECOSYSTEMS *

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ABSTRACT

Three types of periphyton have been distinguished in the littoral of the Mazurian Lakes: 1 — autotrophic type characterized by a clear predominance of plant organisms and often mass, monospecies occurrences of algae, 2 — autotrophic-heterotrophic type characterized by the occurrence of plant and animal organisms in similar quantities and presence of a significant amount of detritus, 3 — heterotrophic type, characterized by the dominance of animal forms and often mass occurrences of Spongia and Bryozoa. The productive and consumptive role of the periphyton in different environments of the lake littoral has been discussed.

INTRODUCTION

The role of a community in the trophic structure of an ecosystem is expressed by the ratio of the production to the consumption intensity in a given community. The majority of aquatic communities is in this respect highly stable. And so as an example in the profundal benthos consumptive processes always prevail and in the littoral and pelagic plankton as a rule the processes of production are greater than the processes of consumption. This problem presents itself quite differently in relation to the periphyton. In the periphyton the plant and animal organisms occur in variable proportions and it results from this fact that in different environments or in different periods production or consumption processes can prevail in this community. Many authors have established the differences in the composition of the periphyton community depending on depth. Duplakov (1933) in his classical elaboration the results of which have been confirmed by other authors, differentiates the areas of phytoperiphyton and zooperiphyton. Sládečkova (1966) describes a varying share of producers and consumers in periphyton on different depth. Meuche (1939) when analysing the periphyton (Bewuchs) of 42 lakes of east Hollstein has differentiated three types of periphyton: plant, animal and detritus types. The author determines the species characteristic of each of these three types and the environment in which it occurs most often.

The occurrence of different trophic groups in the periphyton is stressed also by Young (1945). King and Ball (1966) have differentiated an inorganic sediments, inorganic material produced on site, organic sediments, and autotrophic and heterotrophic production in the periphyton (Aufwuchs) colonizing plexiglass plates placed

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* The term periphyton as used in this paper is defined: organisms both plant and animal colonizing all kinds of submerged substrates projecting above the bottom. The terminological problems were discussed earlier by Pieczyńska (1964).

in a stream. The authors have determined quantitatively these periphyton fractions basing on the determination of the intensity of the colonization of substrate exposed in the horizontal and vertical position and dry weight, ash free weight, and the chlorophyll content of analysed community. As a result of these studies they have established that in the different parts of the stream analysed an autotrophic or heterotrophic production dominate in the periphyton, and also that the part taken by the organic and inorganic sediment in the mass of the periphyton was variable.

AREA OF STUDY

The problem of the trophic structure of the periphyton was analysed in detail in the littoral cvergrown with emergent plants in five Mazurian Lakes.

The following lakes were studied: Tałtowisko (mesotrophy), Mikołajskie and Śniardwy (eutrophy), Lisunie (dystrophy close to eutrophy) and Flosek (dystrophy). Moreover, observations have been made in 26 other lakes that have been discussed in the paper of Pieczyńska (1961). The periphyton colonizing macrophytes, especially reed *Phragmites communis* Trin which represent the dominant substrate suitable for colonization was the main subject of investigations. In some cases periphyton on stones and sticks was also analysed.

RESULTS

The basis for the differentiation of the periphyton types consisted in analyses of the qualitative composition and the number and biomass of the plants and animals. The periphyton was collected from a known surface of substrate. The fresh and dry weight (drying at 105°C) of the whole periphyton, as well as that of the periphyton after the removal of the plant or animal organisms (depending on the proportions of their occurrence) were analysed. The surface area of substrate colonized by periphyton was estimated according to Pieczyńska (1968).

Three trophic types of the periphyton have been differentiated.

1) The autotrophic type of the periphyton. It is characterized by a clear dominance of plant forms (more than 90 per cent of the community biomass). In eutrophic lakes often mass monospecies occurrences of algae can be observed.

2) The autotrophic-heterotrophic periphyton type. It is characterized by the occurrence of plant and animal organisms in similar quantities. Often significant amounts of detritus can be observed.

3) The heterotrophic periphyton type. It is characterized by a clear dominance of animal forms (more than 90 per cent of the community biomass). Often Bryozoa and Spongia occur in mass. In the period of the mass development of these organisms the plant forms do not occur or are less than 1 per cent of the periphyton biomass.

In all the lakes under study in every moment of the study all the three periphyton trophic types were found to occur. The periphyton of the heterotrophic type developed most intensely in the autumn (in the majority of cases this was related to the development of Bryozoa). The autotrophic periphyton type reached the peak of its development in different periods of the

year (except winter). The autotrophic-heterotrophic periphyton type was encountered in all periods of time in a similar quantity.

Among the five lakes analysed in detail the greatest differentiation of the periphyton was found to occur in the Lake Śniardwy which is characterized by the differentiated littoral zone. The lowest variability of the periphyton was observed in dystrophic lakes (Flosek and Lisunie). In these lakes the periphyton was poorly developed and in the majority of cases it represented the autotrophic-heterotrophic type. The Mikołajskie Lake and Lake Tałtowisko were characterized by a similar periphyton variability.
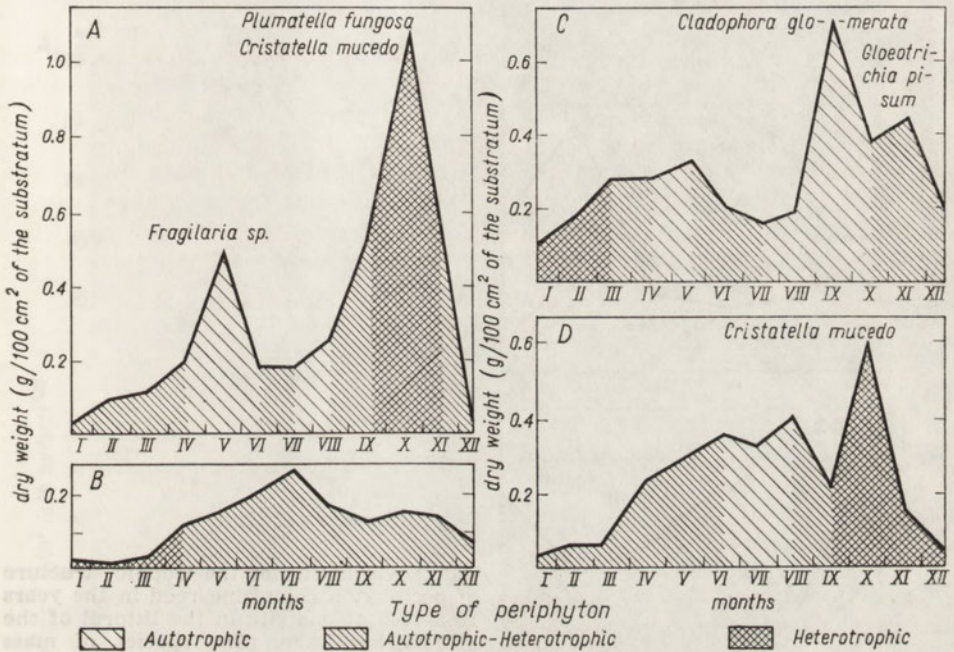
Fig. 1. Trophic structure of periphyton colonizing reed at several sites in the Mikołajskie Lake in 1964. (The species of mass appearance are given). A–D = several sites

In the most intensely studied Mikołajskie Lake the variability of the trophic types of periphyton was analysed in a year's cycle, in different places of the lake and in the consequent years of studies on the same place. The following facts have been ascertained:

1) During the same period of time in different sites of the lake different periphyton types are found to occur (Fig. 1).

2) In a year's cycle the periphyton type in a given site can change several times with the restrictions that the heterotrophic periphyton type occurs most often in winter and in autumn (Fig. 1).

3) In subsequent years of studies in the same seasons and in the same site, different periphyton types can be found to occur. The variability of the occurrence of the heterotrophic periphyton types can be related to the cyclic occurrence of Bryozoa (Fig. 2).
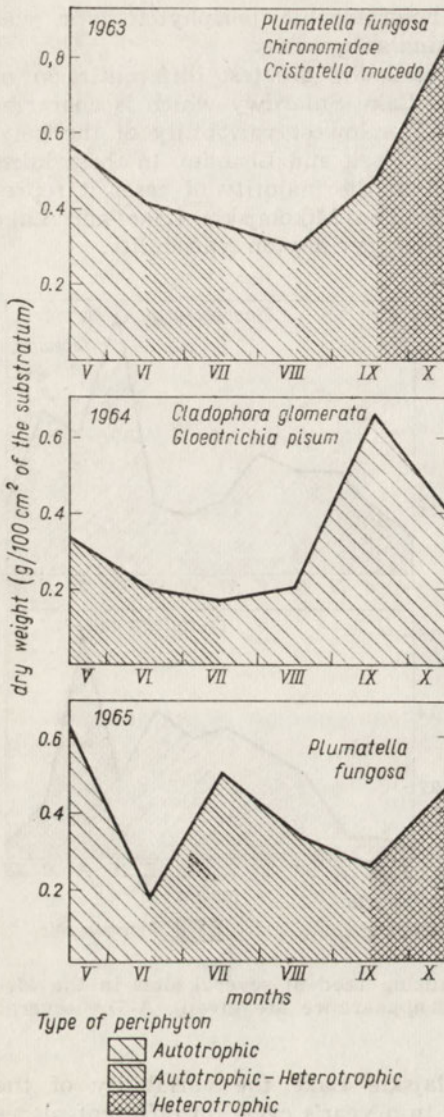
Fig. 2. Variability of the trophic structure of periphyton colonizing reed in the years 1963–1965 at one site in the littoral of the Mikołajskie Lake. (The species of mass appearance are given)

In the periphyton of the Mikołajskie Lake, as it has been previously ascertained (PIECZYŃSKA 1965), often mass, monospecies occurrences of plant and animal organisms can be observed. When analysing the trophic structure of the periphyton in the majority of cases the peaks of the biomass of the periphyton have been found to occur during mass, monospecies occurrences. Most often Bryozoa (*Plumatella fungosa* and *Cristacella mucedo*) were encountered as well as algae (*Gloeotrichia pisum*, *Cladophora glomerata* and *Fragilaria* sp.). The autotrophic-heterotrophic periphyton type reached usually a much lower biomass (Fig. 1 and 2).

Besides the analysis of the differentiation of the trophic periphyton types

the periphyton of the littoral covered with emergent plants in the Mikołajskie Lake has been evaluated as a whole. In year 1964 the biomass and composition of the periphyton was analysed every month or every two weeks in places situated in different parts of the water body. Simultaneously the surface area of substrate colonized by the periphyton was determined in order to obtain the information concerning the quantity of periphyton in this zone of lake. The periphyton in the Mikołajskie Lake reaches its development peak in summer and autumn (Fig. 3B), and occurs in significantly smaller quantities in winter and early spring. The quantity of periphyton is related to the intensity of its development as well as to the variations of
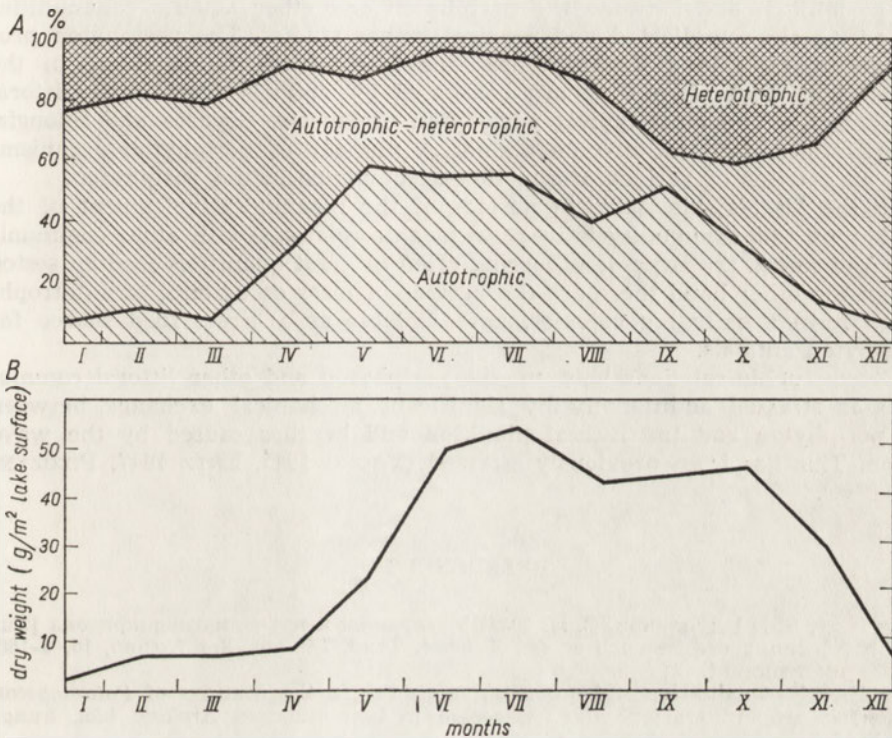
Fig. 3. Trophic structure and biomass of periphyton in the Mikołajskie Lake in 1964. Littoral overgrown with emerged vegetation. A — Trophic structure of periphyton, B — Periphyton biomass

the substrate area suitable for colonization (this problem was previously discussed — PIECZYŃSKA 1968). The spring increase of the periphyton biomass is the result of the intense development of periphyton organisms as well as of the mass growth of young reeds that are the substrate for the periphyton organisms.

When determining the periphyton in the Mikołajskie Lake littoral with emergent plants as a whole, it has been found that the autotrophic-heterotrophic type prevails. The prevalence of the autotrophic periphyton type has been found to occur in the summer period (Fig. 3A). As this is the period of

the maximum biomass of the periphyton it can be said that in the analysed environment the productive role of the periphyton prevails over the consumptive role of this community.

The value of the primary production of periphyton in relation to the production of other communities of the littoral zone covered with emergent plants in the Mikołajskie Lake has been evaluated simultaneously (Pieczyńska and Szczepańska 1966). It has been established that the periphyton production is 23 per cent of the yearly net primary production (macrophytes 57 per cent, plankton 20 per cent).

The analysis presented here gives only a general impression of the role of the periphyton in the lake trophic structure. The trophic relations within the periphyton and between the periphyton and other aquatic communities are extremely complicated and require further studies. The periphyton producers are only to a limited extent the food of the fauna living in the periphyton, most often they are consumed by animals from other littoral communities. The most typical periphyton organisms, Bryozoa and Spongia, the filtrators, feed in turn on seston. A number of periphyton organisms feed on detritus of various origin, that accumulates in the periphyton.

In the Mikołajskie Lake, in periods of the maximal development of the periphyton this community is in close trophic relations with other communities. And so e.g. the Bryozoa occurring often in great quantities feed on seston but on the other hand there are the periods of mass occurrence of autotrophs which form usually big colonies, not available as a direct food source for periphyton animals.

Close trophic relations between the periphyton and other littoral communities is stressed additionally by significant mechanical exchange between the periphyton and the littoral plankton and benthos caused by the wave action. This has been previously stressed (Young 1945, Entz 1947, Pieczyńska 1964).

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THE MEASUREMENT OF RESPIRATORY RATES UNDER FIELD AND LABORATORY CONDITIONS DURING AN ECOLOGICAL STUDY ON ZOOPLANKTON

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ABSTRACT

Two procedures adopted in an attempt to measure the respiratory rates throughout the year of the naturally composed macro-zooplankton in near-field conditions are described critically and in detail. Some results are presented showing the changes in the oxygen consumption per mg dry weight of the larger zooplankton from two reservoirs in the lower Thames Valley (England). An attempt is made to compare the levels of "field" respiratory rates per 5 l of the zooplankton during a period when *Daphnia hyalina* predominated with the levels obtained when laboratory respiratory rates of this species were applied to its field population numbers obtained during the same period.

INTRODUCTION

In ecological studies, the measurement of respiratory rates can provide us with information difficult to obtain in other ways, namely, how much energy is required for maintaining normal activities in a particular species and, together with measurement of growth rates, gives us another estimate of the demands this species-population makes upon its food supply, in addition to a direct one. The respiratory rate is also an extremely sensitive measure of the physiological state of an animal and its measurement helps us to distinguish the different states of metabolism exhibited by animals throughout their life cycle in response to various environmental conditions. Some ecologists have suggested that it is not necessary to measure respiratory rate to the degree of sensitivity possible because the range of metabolic levels in any species is too small for the type of productive studies with which most International Biological Programme investigations are concerned. However, if our aim is not only to produce some value or other representing the secondary biological production in terms of cal/m² year but also to understand why this particular value was obtained and therefore to be able to predict future values, more needs to be known about the patterns of both metabolic and growth responses of different species to their environment.

It is well known that the metabolism of animals is affected by various environmental conditions such as temperature, food concentration and qua-

lity as well as the state of development and body size of the species itself.
It may also be that an animal's previous history affects its respiratory res-
ponses to its present environmental conditions. In 1966, BLAŻKA gave a very
interesting paper in which he suggested that the relationship between the
rate of oxygen consumption and temperature was not a simple one of tem-
perature acclimatization. He postulated three types of metabolic regulations
related in some way to food conditions which occurred in some species of
the cladoceran genus Daphnia and perhaps in other crustacea; in two of
these, the level of metabolism did not alter under the influence of immediate
environmental change but required some time. The first of these metabolic
regulatory mechanisms was revealed during a period of low winter meta-
bolism in *Daphnia hyalina* coinciding with low concentrations of seston (less
than 3 cal/l); the respiratory rate decreased proportionately to the seston con-
centration so that the energy reserves of these winter daphnids could last
for 6–7 weeks longer. The resumption of the spring-summer levels of meta-
bolism did not take place immediately but only after about 6–8 weeks or two
or three generations. The second type of metabolic regulation is concerned
with the variability of the relationship between oxygen consumption and
temperature; this was detected in several daphnid species, all with similar
responses. Measurement of the metabolic rate per mg body N at several tem-
peratures from 5°–30°C at different seasons of the year in field animals as
well as in well-fed laboratory cultures kept at 20°C showed that the pattern
of metabolic response was different in field animals at different seasons and
was different in the laboratory and field animals. BLAŻKA suggests that the
field animals were exhibiting a more developed temperature acclimatization.
The third type of metabolic regulation postulated concerns the varied per-
centage utilization of protein as a respiratory fuel under different levels
of diet. Information about this was obtained by measuring the quantity of
ammonia excreted as well as oxygen consumed and by assuming that all the
ammonia excreted came from catabolized protein. In laboratory cultures of
D. hyalina with a surplus of food, proteins were not used as a source of
energy whereas in the field, between 12–80% of the liberated energy came
from protein metabolism. The percentage of protein metabolized in this way
was affected by environmental factors, being increased with increase in
temperature and decreased by an increase in the level of food.

If BLAŻKA's ideas are correct and the previous nutritional history of an
animal can affect its present responses to its environmental conditions, direct
measurements of metabolic rates of field animals under field or simulated
field conditions may enable us to detect this situation, to interpret the pat-
tern of metabolic response to seasonal and other changes in its normal envi-
ronment as well as to gain some idea of the degree of metabolic variation to
be expected. During the last three years, an attempt has been made to mea-
sure the oxygen consumption of the naturally composed macro-zooplankton
(retained on a 0.3 mm mesh) in as near to field conditions as possible in order
to determine whether any pattern of variation in metabolism was detectable.
This work was part of a study on the metabolism and secondary production
of the zooplankton in three reservoirs of the lower Thames Valley whose
phytoplankton was being investigated simultaneously (STEEL et al., in pre-
paration).

METHODS

For field measurements of respiration at all seasons of the year, only the simplest, weather-proof apparatus can be employed. Simple glass stoppered flasks of 300 ml capacity protected in nalgene tubes were used, flushed and filled with reservoir water, to which were added concentrated suspensions of zooplankton filtered off through a 0.3 mm mesh from a quantitative sample. After fixation with an azide modified alkali-iodide solution, the level of dissolved oxygen was determined by the standard Winkler titration, using 50 or 100 ml sub-samples and an 0.0125 N sodium thiosulphate solution. The level of dissolved oxygen in the animal flask was compared with that of two control flasks without animals, one of which, the initial control, was fixed immediately after filling and the other, the final control, at the same time and having received the same treatment as the animal flask; the difference between the animal and final control flasks was used to calculate oxygen consumption by the zooplankton concentrate. These two controls were important in that they provided a check on the oxygen changes occurring associated with the water medium itself. The flasks were suspended in the water body itself, which thus acted as a natural water bath, usually from a buoy or raft whose wind-induced movements provided some shaking. The term, "in as near to field conditions as possible" refers mainly to temperature, the water medium used and to the period of time between the collection of animals and their re-suspension inside bottles.

Two procedures were developed during the course of the study differing in the methods employed to collect the animals (nets hauled vertically from above the bottom to the surface or volume samples taken from various depths) and in the length of exposure period (24 or 4hr); the consequences of these technical differences are described below.

The earlier procedure was developed in 1966—1967 by CREMER, whose aim was to study comparatively the seasonal changes in numbers, biomass and metabolism of the zooplankton of three reservoirs. The sampling and subsequent treatment of samples is described in more detail in CREMER and DUNCAN (1969) and was designed to provide composite collections consisting of a known number of vertical net hauls from several stations. These composite samples were considered to be representative of the water body as a whole, leaving in abeyance for the moment the question of how selectively nets sample a column of water. The net samples were convenient in that they provided an integrated sample of what was present throughout the depths. In the laboratory, the composite samples were split into equal sub-samples, using a plankton splitter designed by MOTODA (1959) and these were used for either counts and species analysis, dry weights of various components or respiratory measurements. The respiratory sub-sample was treated carefully and immediately; it was further sub-divided to provide suitable concentrations of animals whose oxygen consumption was not more than 20% of the initial oxygen concentration. It was a matter of experience to judge this, especially as the degree of sub-sampling necessary varies seasonally. Thus in May, during the peak daphnid numbers, too large a sub-sample was used resulting in a greater than 20% decrease in oxygen concentration in the animal flask so that these results had to be rejected. As the exposure period was 24 hours in order to encompass any diurnal variation, it was necessary

to use reservoir water filtered through a glass fibre pad (*GF/C*) to remove the algae and bacteria; the use of filtered water meant that the animals had no food available while in the flasks. The two control flasks were also filled with filtered water and the differences in oxygen concentration was usually less than 30% of the animal oxygen consumption. The animal and final control flasks were suspended, undarkened, from a buoy in a windy part of the reservoir near the laboratory for 24 hours. As the oxygen consumption of the macro-zooplankton was obtained by subtracting the oxygen content of the final control from that of the animal flask, any heightened initial respiration due to the disturbance of the animals by handling will be incorporated in the results, although this error is somewhat reduced because of the long exposure period; KAMLER (1969) has recently drawn attention to this error associated with closed-bottle-Winkler respirometers. To what extent lack of food for 24 hours affects the oxygen consumption of these animals is not known.

During this work, an attempt was made to estimate the oxygen consumption of not only the naturally composed zooplankton but also of its component fractions, namely the copepods, consisting of the larger copepodites and adult of *Diaptomus gracilis* and *Cyclops* spp., and the cladocerans, consisting of *Daphnia hyalina,* other species of Daphnia and the larger stages of *Bosmina longirostris.* It is possible to separate the copepods from the rest of the zooplankton by STRASKRABA's narcotic technique (STRASKRABA 1967) and to measure their oxygen consumption in a separate flask and to calculate the respiration of the cladocerans by subtraction. The effect of the mild narcotization on the respiratory rate of the copepods has not yet been tested but the animals recover very rapidly their normal swimming movements. However, the subsequent shaking to separate off the cladocerans is likely to produce a period of initial "disturbed" respiration as mentioned above.

The second procedure was developed during 1967 and 1968 by DUNCAN on one of the three reservoirs and on another during 1968 and 1969 by ANDREW. In contrast to the procedure described above, the concentration of animals suspended in the flasks was determined by the number of animals collected by the five litre PATALAS volume sampler (PATALAS 1954) and retained on a 0.3 mm mesh net disc. Moreover, all the handling of animals, from their collection to their re-suspension inside the flasks, was carried out under field conditions, as shown in Fig. 1. The period of exposure was only four hours. Animals from a known depth were washed into a flask which was then flushed out with three times its own volume of coarse filtered reservoir water from the same depth. This coarse filtered water contained all the particles or organisms which passed through the 0.3 mm mesh net disc, so that some food was available for the herbivorous species. However, due to the presence of algae, detrital particles and smaller zooplanktonic organisms, it was necessary to darken the flasks to prevent photosynthetic production of oxygen and to expose the flask for a period too short for bacterial respiration to reach a measurable level. The difference in the oxygen concentration of the initial and final controls was greater than in the first procedure when glass fibre filtered water was used, and was between 50–100% of the animal oxygen consumption for most of the year but dropped to 25% with a mean value of about 10% during peak daphnid periods. Rather than acting as a control on the changes occurring in the water medium, these differen-

ces provided an estimate of the oxygen consumption of the various organisms present, which passed through the 0.3 mm mesh. The oxygen consumption of the macro-zooplankton was calculated from the difference in oxygen content of the final control and the animal flask and will include both the initial period of heightened respiration due to disturbance and possibly darkness as well as any possible effect which the presence of animal excretory products may have on algal or bacterial respiration. The former error will be more serious than in the first procedure since it will form a greater proportion of a four hour consumption. It may be possible to eliminate by fixing an additional animal bottle after the period of disturbance, previously determined. Duplicate samples were taken at 2 m intervals down to 9 m depth or to the thermocline at weekly or fortnightly intervals.
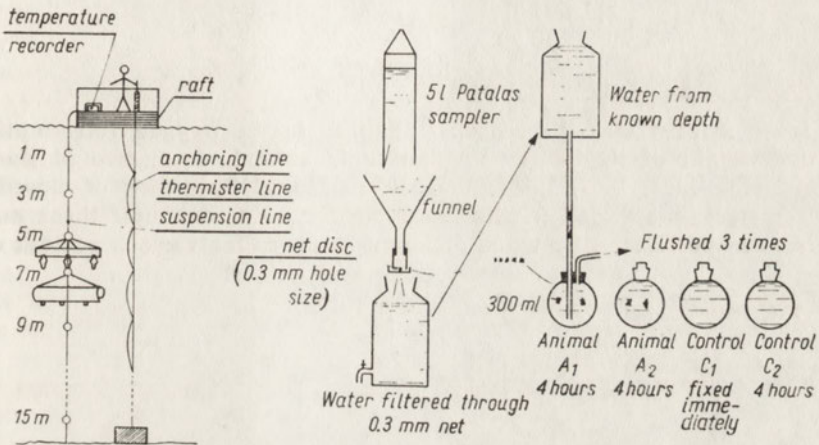

Fig. 1. Diagram showing the collection, handling and suspension of samples for "field" respirations

The time taken between the removal of animals from the reservoir to their re-suspension inside the flasks was much shorter in the second procedure. Usually all the titrations were completed on the same day and the animals filtered off to determine their dry weights. Thus it was possible to obtain quite quickly an estimate both of the standing crop and the metabolic intensity of the macrozooplankton, which is useful during periods of rapid change. Parallel samples were also taken for counts and species analysis.

One of the problems not yet solved satisfactorily is how to fix the oxygen in the animal flask. Direct fixation in the presence of the animals is the simplest technique which can be easily carried out at the edge of the reservoir; this does not seem to affect the precision of the titration carried out within an hour, ± 0.026 ml thiosulphate for a 50 ml sample, but does alter its accuracy (Andrew, personal communication). The error which is 0.013/1 ml thiosulphate/mg dry wt. animal is the result of loss of iodine either because the manganic hydroxide which is trapped in or on the carapaces is not all dissolved on acidification or because it colours the animals' bodies and is isolated from the titration. An alternative method attempted during this work was to siphon off a sub-sample into a smaller bottle, filtered through

a coarse mesh disc to remove the animals. This produced rather variable results when performed at the edge of the reservoir because of the problems of preventing contact with air, of flushing the receiver bottle adequately to remove the film of air on its surfaces and of clogging of the netting by animals forced against it by water flow. It may be possible to use a syringe to withdraw a good sub-sample, especially if it is simultaneously fixed as in the Fox and Wingfield technique, although this method precludes any previous flushing of the syringe walls. The addition of liquid paraffin does not ensure isolation from atmospheric air and contaminates the bodies of the animals whose dry weights are desired. Transporting the flasks for fixation under laboratory conditions involves submerging them in water containers to prevent air diffusion through the ground glass joint, demands more labour, lengthens the exposure period and risks changes in temperature.

RESULTS

Figure 2 illustrates the seasonal changes in the oxygen consumption per mg dry weight of the larger zooplanktonic animals from two of the reservoirs during 1966, 1967, 1968 and 1969, measured by means of closed bottle respirometers, suspended in the reservoir for 24 or 4 hours; these measurements were performed by three different workers for various periods of time
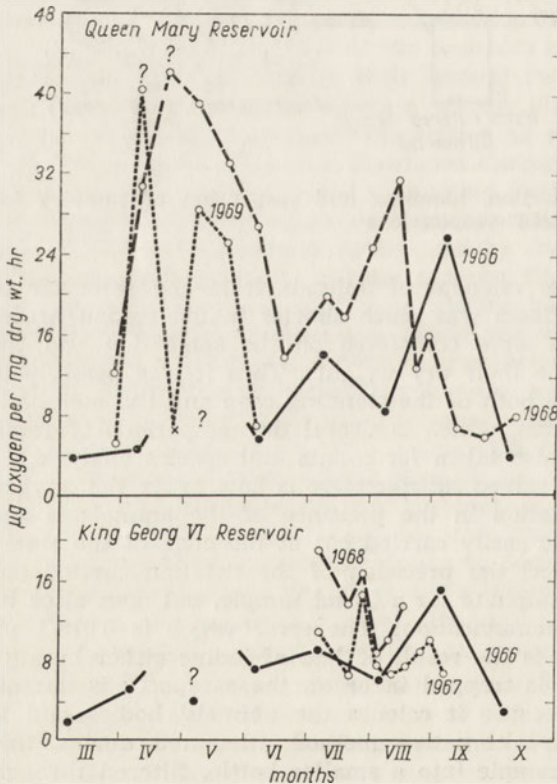

Fig. 2. Seasonal changes in the oxygen consumption per mg dry weight of macro-zooplankton from two reservoirs in 1966–1969

at monthly, fortnightly or weekly intervals. Although there is considerable variation in the maximal absolute values of metabolic rate in different years for the same reservoir, these are probably not real but reflect procedural and calculation differences associated with different exposure times, errors due to disturbance from handling, darkness, absence of food. What is striking is the similar seasonal pattern of variation in metabolic intensity revealed in consecutive years with the periods of more intense metabolism occurring during the spring, in the summer and again during the autumn. The causes of some of these periods of more intense metabolism are not yet known, although in Queen Mary Reservoir, the spring period coincides with a period of intense parthenogenetic reproduction by *Daphnia hyalina* resulting in very large standing crops of very young, small animals with a high level of weight specific respiratory rate. However, this is not the cause of the periods of more intense metabolism later in the year. Nor are these caused by the higher water temperatures prevailing at this time but rather they seem to be associated with changes in the specific composition of the zooplankton (with relatively few *Daphnia hyalina*, relatively more *Bosmina longirostris* and the appearance of considerable numbers of adult cyclopoids) and in their breeding conditions (a greater proportion of female *Diaptomus gracilis* bearing egg sacs). This is discussed in more detail in CREMER and DUNCAN (1969) but clearly more information is required about the respiratory rates of different developmental stages of these species in order to interpret the complex changes occurring in the summer and autumn.

The level and quality of food available is also likely to affect the metabolism of zooplanktonic animals. This would be best demonstrated by the direct measurement of ingestion and assimilation rates together with respiratory rates and some information on the percentage utilization of protein as a respiratory fuel, as suggested by BLAŻKA (1966); the simultaneous and frequent measurement of these would be most indicative of the food situation but difficult to achieve. However, the juxtaposition in Fig. 3 of the seston concentration, level of zooplankton biomass (predominantly cladoceran) and its weight specific respiratory rate during the summer of 1968 in the top 5 m of King George VI reservoir suggests that the overall decline in metabolic intensity of the zooplanktonic biomass may be a reflection of the dramatic decline in seston level. The alternation at almost weekly intervals of periods of high biomass levels and lower metabolism (19.VII, 1.VIII) with lower biomass levels and more intense metabolism (4.VII, 26.VII and 8–15.VIII) coincides with the occurrence in the zooplankton of either predominantly large or predominantly small daphnids.

During the spring 1968, an attempt was made to compare the respiratory rates of the zooplankton in Queen Mary reservoir obtained in two ways. The spring period was chosen because at this time the zooplankton consists mostly of *Daphnia hyalina* reproducing most intensely and resulting in its highest levels of standing crop biomass and numbers. What was compared was the mean respiratory rate of zooplankton from 5 l samples from different depths as measured in closed bottle respirometers suspended in the reservoir with rates calculated from respiratory rates of different sizes measured in the laboratory applied to the same field populations.

In the laboratory, the progeny from several large, old females containing twenty or more parthenogenetic eggs were kept separate at 20°C in condi-
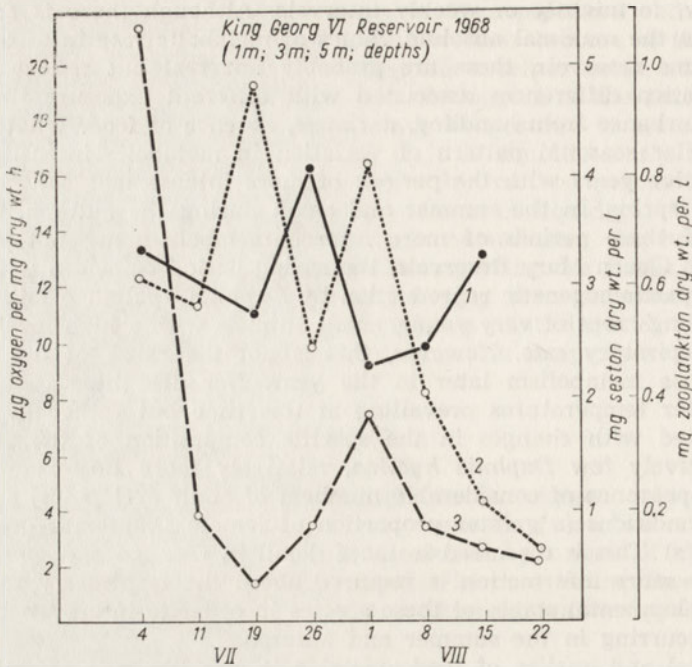
Fig. 3. Changes in the concentration of seston biomass and the oxygen consumption per mg dry weight and biomass of macro-zooplankton in one reservoir during the summer 1968. 1 — zooplankton metabolic rate, 2 — zooplankton biomass, 3 — seston biomass

tions of surplus food which was *Oocystis* spp. cultured from the reservoir populations. These old females were the precursors of the subsequent spring daphnid "bloom". The temperature was 20°C because it was the first temperature investigation to be completed in a programme studying the influence of temperature on the respiration and development of *D. hyalina*. The young released from these older females were individually named and their development followed in individual cultures until they died. Fourteen such individuals were successfully reared in dishes whose 30 ml filtered reservoir water was changed daily and replenished with surplus food. The following daily observation was made on each individual: growth as length in mm from the top of the helmet to the inflexion at the base of the spine; respiratory rate in the modified cartesian diver (ZEUTHEN 1950, KLEKOWSKI 1968); the occurrence of ecdysis; the reproductive state, involving the condition and size of ovary, the number of eggs and developmental state of the embryos. Figure 4 illustrates the developmental cycle of animal 11c which lived for 600 hr at 20°C up to its 10th instar when it had produced 6 broods of eggs. Such a method of investigation pioneered by Dr. R. Z. KLEKOWSKI in the study on *Macrocyclops albidus* (Jur.) (KLEKOWSKI and SHUSHKINA 1966) provides a pattern of both the individual's and the species' life history. Thus 11c missed producing a brood of eggs during its 7th instar, for some reason, and this coincided with both a period of respiration lower than expected (horizontal hatching) and a cessation of growth in length; the stippled areas re-
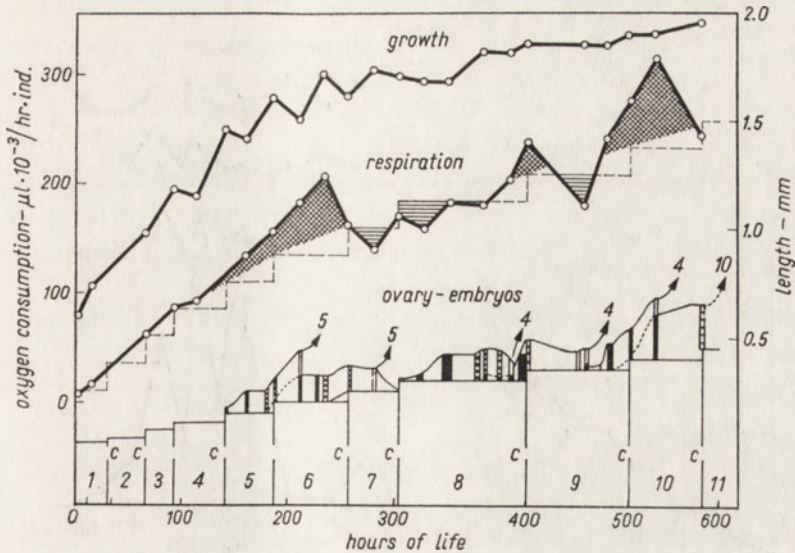
Fig. 4. The length, oxygen consumption, ecdysis and reproductive state of an individual *Daphnia hyalina* (number 11c), cultured at 20°C, fed on *Oocystis solitaria* and observed at daily intervals throughout its life span of 600hr. C — carapace instars

present the increased respiration associated with the development of an ovary and its released eggs and embryos.

For the purpose of the present comparison of metabolic rates, these fourteen life histories were employed to obtain average individual respiratory rates at 20°C for different length classes. Figure 5a illustrates the relationship between the mean oxygen consumption per hour of an individual and body length and Fig. 5b presents the numbers of different length classes of *D. hyalina* present in Queen Mary reservoir during April, May and June 1968. From these two sets of data was calculated the total oxygen consumption of the *D. hyalina* present in five litres, both at 20°C and at field temperature (whose values are given on the lower axis); the measurements at 20°C were converted to field temperatures by means of the tables based on Krogh's normal curve as published in WINBERG (1956). The two population respirations, derived from laboratory measurements applied to field numbers, are illustrated in Fig. 6 along with the field respirations per 5 l measured by means of closed-bottles suspended in the reservoir; this latter curve gives also the range of the 95% confidence limits.

Figure 6 shows that the field respirations during this period of the daphnid spring peak were considerably higher than the population respirations derived from laboratory measurements but the similar shape of the two sets of curves suggests that the same events are being described. The reasons for this difference is not known at present. It is unlikely to be due to the respiration of the other species present in the field bottles since these were not numerically abundant during this time; the mean numbers per 5 l of larger zooplanktonic species between 25.III.68 and 17.VI.68 was 131 for *D. hyalina*, 18 for *Cyclops* sp., 10 for *Diaptomus* sp. and 1 for *Bosmina* sp. As mentioned
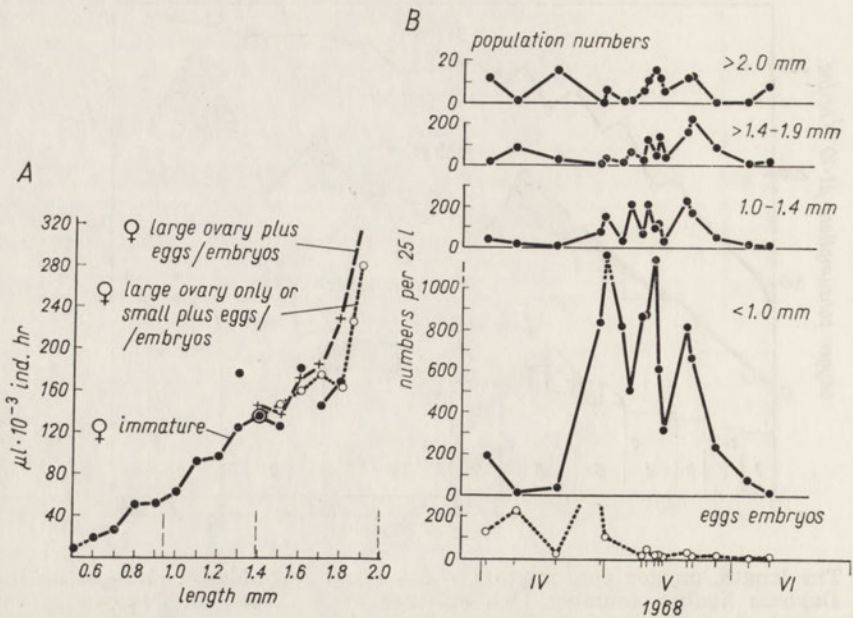
Fig. 5. A — the mean oxygen consumption of 14 *Daphnia hyalina* cultured at 20°C, the relationship between oxygen consumption and body length. B — the numbers per 25 l of *Daphnia hyalina* of different sizes in one reservoir during the spring 1968
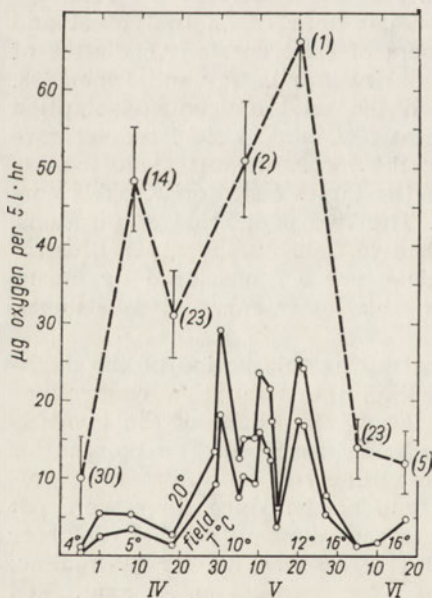
Fig. 6. A comparison of the "field" and laboratory respiration of zooplankton from Queen Mary reservoir, 1968, during a period when *Daphnia hyalina* was predominant. The methods compared were the closed-bottle-Winkler respirometer and cartesian diver respirometers. - - - field respiration at field temperature of zooplankton — mostly *D. hyalina* (± standard deviation. Numbers in brackets — ml space per daphnid); ——— laboratory respiration of *D. hyalina* applied to field populations of *D. hyalina*

earlier, any initial heightened respiration due to disturbance from handling is incorporated in the field respirations but has been excluded from the diver results which were applied to population numbers; this is a possible cause of the difference not yet measured. Another possible cause is the effect of crowding; ZEISS (1963) records that adult *Daphnia magna* confined to a space of 0.24 or 0.12 ml/individual consumed 2 to 2.5 times more oxygen at 19–21°C than those with 12 ml available per individual and, on this basis, criticises the use of microrespirometers for the measurement of daphnid respiration. The space available per daphnid is given in ml/individual in Fig. 6 (the numbers in brackets) and varied throughout the spring period. It is clear that it was minimal (between 1 and 2 ml/individual) during the greatest respiration, however, the space available for single daphnids of various ages in the cartesian divers used was between 0.01 and 0.02 ml and the respiratory rates when applied to population numbers revealed lower levels of respiration per 5 l rather than higher. An important difference between the two respirometers was the possibility for active movement; all sizes of animals in the bottles but only the smaller daphnids in the divers could swim actively during the respirometric measurements. Moreover, in both respirometers, the period of measurement lasted about 4 to 5 hours which may be a long time for a daphnid to be without food, as was the situation in the divers, whereas normal food in reduced concentration was present in the field bottles. Clearly, further investigation needs to be undertaken in order to determine the causes of the difference in level revealed in Fig. 6.

SUMMARY

1. Two procedures adopted in an attempt to measure the respiratory rates throughout the year of the naturally composed macro-zooplankton in near-field conditions are described critically and in detail. Both procedures involved the use of concentrates of zooplankton and closed-bottle-Winkler respirometers but differed in the presence or absence of food and in the duration of exposure (4 or 24 hr).

2. Some results are presented showing the changes in the oxygen consumption per mg dry weight of the larger zooplankton from two reservoirs in the lower Thames Valley (England) at different seasons of the year and during a period of rapid decline in the summer seston concentration. The possible causes of the changes revealed are discussed.

3. An attempt is made to compare the levels of "field" respiratory rates per 5 l of the zooplankton during a period when *Daphnia hyalina* predominated with the levels obtained when laboratory respiratory rates of this species were applied to its field population numbers obtained during the same period. The laboratory measurements were obtained from daily measurements throughout the life cycle of fourteen *D. hyalina*, cultured at 20°C and fed on *Oocystis solitaria* by means of Zeuthen's stoppered cartesian diver, an approach pioneered by KLEKOWSKI in *Macrocyclops albidus* Jur. (KLEKOWSKI and SHUSHKINA 1966). The pattern of changes in the population respiratory rate throughout this period of spring peak abundance given by the two methods was very similar but the levels differed. Possible causes of this difference are discussed.

R. Z. KLEKOWSKI for so generously passing on his experience both in the techniques of the Zeuthen stoppered cartesian diver and in its application to ecological problems.

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RELATIONS BETWEEN THE FOOD CONCENTRATION, FILTRATION RATE AND EFFECTIVENESS OF OXYGEN UTILIZATION BY CLADOCERA

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ABSTRACT

The interrelation of the regression used hitherto (filtration rate on food concentration) and the efficiency of O_2 utilization was discussed. At low food concentrations the filtration rate is sufficiently high to permit the Cladocera to satisfy their demand for energy, the oxygen utilization efficiency being then extremely low. At high food concentrations the filtration rate attains the minimum but remains sufficiently high to satisfy the demand for oxygen, the efficiency of oxygen utilization being then at its physiologically possible maximum for the given species. The respective empirical formulae connecting the above parameters are given and discussed.

Relations that exist between the filtration rate and food concentration among Cladocera has adequately been examined. To the most important works belong those written by SUSHCHENYA (1958, 1964), MANUYLOVA (1958), MONAKOV and SOROKIN (1961), SHUSHKINA and PECEN (1964), RICHMAN (1958), BURNS and RIGLER (1967), RIGLER (1967), and others. Nevertheless, all these works deal with the filtration barely as with a source that supplies the animals with food. In contrast to this, Cladocera that let water through their filtration apparatus take not only food, but also oxygen necessary for their respiration processes. The existing relation between the filtration rate and food concentration in the surroundings may be explained only after a comparison of the data concerning both feeding and respiration of animals.

A general character of the curve that reflects such a relation is known satisfactorily (SUSHCHENYA 1964, JORGENSEN 1966). Where the food concentration is less than 0.2 mg of dry wt./l the filtration rate is constant, shows its maximum and corresponds to a particular rate, at which the individual species let water through their filtration apparatus. In the surroundings, where the concentration ranges from 0.2 to about 15–20 mg of dry wt./l, the filtration rate depends upon the food concentration. It should be emphasized here that with the increase in food the filtration rate becomes constant again. It is known that aquatic animals are able to use only part of the oxygen dissolved in water that flows through their incurrent siphons (PROSSER and BROWN, 1962).

Let the effectiveness of oxygen utilization be U_q, then

$$U_q = \frac{Q}{F \cdot M_{O_2}} \qquad (1)$$

where:

Q — respiration in mg O_2 per 1 time unit,
F — filtration rate in ml per the same time unit,
M_{O_2} — oxygen contents (mg/ml).

In other words, Q is the demanded amount of oxygen dissolved in water that passed through the incurrent siphon; and FM_{O_2} — the total amounts of oxygen in the given water volume.
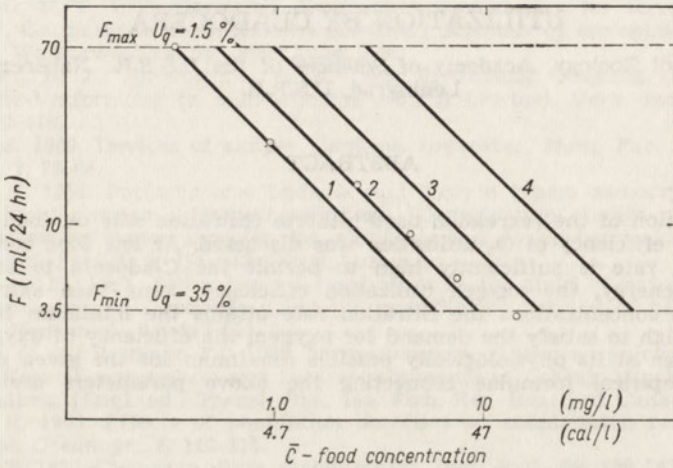
Fig. 1. Dependence of filtration rate (F) upon mean food concentration ($\overline{C}$). Filtration rate calculated according to formula (6) for a crustacean 0.032 mg in weight (dry weight. $1 - 1/U = 50^0/o$, $2 - 1/U = 30^0/o$, $3 - 1/U = 15^0/o$, $4 - 1/U = 5^0/o$. Points on figure: filtration rate of *Daphnia pulex*. Weight 0.032 mg (MONAKOV and SOROKIN 1961)

Figure 1 shows that the value of the oxygen utilization is closely related to the filtration rate (Table I and II). Where food concentration is low and constant, the filtration rate shows its maximum, U_q is constant and equal to 1–1.5%. When the food concentration increases, U_q rises too, since the filtration rate decreases. Partially, the increase in food concentration is compensated by a decrease in its assimilability $1/U$. So, when the amount of food in water decreases about 20 times, both F and U_q decrease about 9 times (according to BURNS and RIGLER 1967). The maximum value of U_q is noted after the filtration rate becomes constant again; then, the whole U_q is equal to about 30–35%. We may assume that any additional decrease in filtration rate is impossible, mainly due to a limited ability of Cladocera to use more oxygen from water. Thus, the conditions of food surplus are analogous to those of oxygen deficit.

The data obtained during the experiments allowed the author to present a dependence of the value U_q upon the food concentration (Fig. 2). Unfortunately, insufficient studies on the filtration rate, under conditions where the food

Table I. Relation between the food concentration and use of oxygen from filtrated water. The value U_q calculated by the author, F and U — according to MONAKOV and SOROKIN (1961). It has been accepted in these and in the other calculations that the oxygen content is equal to 7 mg/l, water temperature being 20°C

Species and live weight in mg	$\overline{C}$ mg of dry weight in 1 l	$1/U$ %	F ml/ind. per day	F/Q ml/mg O_2	U_q %
Daphnia pulex	0.30	33.2	64	8700	1.6
0.320	0.79	47.5	24	3250	4.4
	1.92	44.2	15.8	2140	7.2
	4.12	32.6	9.5	1280	10.6
	6.60	33.5	5.4	730	19.5
	14.30	17.8	3.0	400	35.2
Daphnia pulex	1.1	9.4	6.3	1940	7.4
0.120	2.0	13.9	3.1	950	14.5
	5.3	13.7	3.1	520	27.5
	9.7	8.56	2.4	740	19.4
Daphnia	1.2	—	14.0	4700	2.5
longispina	3.1		7.0	2350	4.9
0.120	7.4		4.1	1370	8.4
	11.2		2.88	960	12.0

Table II. Relation between the food concentration and oxygen utilization from filtrated water by *Daphnia rosea* (according to BURNS and RIGLER 1967)
Live weight — 0.290 mg, oxygen contents in water — 7 mg/l, temperature — 20°C

Food concentration — C		F ml/ind. per day	U_q %
10^5 cells/ml	mg of dry weight/l		
0.25	0.5	42	2.1
0.50	1.0	28.6	3.0
0.75	1.5	26.4	3.25
1.00	2.0	21.6	4.0
1.50	3.0	16.8	5.1
2.00	4.0	12.0	7.15
4.00	8.0	7.2	12.0
5.00	10.0	4.8	18.0

concentration in water was 20 mg of dry wt./l, did not give any possibility to show exactly the superior limit of the value U_q. However, the following may be thought to be the first working formula presented as an exponential function of the following type:

$$U_q = A \cdot \overline{C}^{\alpha}$$

at the concentration from 0.1 mg/l to 3 mg/l:

$$U_q = 3.7 \overline{C}^{0.58} \qquad (2)$$

at the concentration from 3 mg/l to 20 mg/l:

$$U_q = 2.9 \overline{C}^{0.84} \qquad (3)$$

11*

Table III. Comparison of filtration rates calculated according to

Author, year	Species	Dry weight $(mg \cdot 10^{-3})$	$T+P$ $mg \cdot 10^{-3}$/ind. per day	Q $mgO_2 \cdot 10^{-3}$/ind. per day
Sushchenya 1958	Diaphanosoma brachyurum	5.3	2.6	1.95
	Daphnia magna	130	34	26
	Simocephalus vetulus	90	22	16
	Bosmina longirostris	2	0.6	0.50
Richman 1958	Daphnia pulex	1	0.36	0.24
Manuylova 1958	Daphnia longispina	8.3	2.7	1.8
	Daphnia cuculata	5.5	1.8	1.2
	Simocephalus vetulus	12.0	4	2.5
	Bosmina coregoni	10.0	3.5	2.3
Shushkina and Pecen 1964	Daphnia longispina	11.6	3.5	2.3

Using (2) and (3) we may calculate the filtration rate (under conditions of a given food concentration) that permits Cladocera to satisfy their demand for oxygen.

There are three methods of calculating the filtration rate considered:

1. There are some formulae that may be used for calculation of filtration rates observed during the examination. To the commonest formulae belongs that of Gauld:

$$F' = V \ln \frac{C_0}{C_t} \qquad (4)$$

Restrictions in applying this formula are discussed in detail by Rigler (1967).

2. The filtration rate may be calculated also on the basis of food demand by Cladocera. The fundamental equation of the energy balance is as follows:

$$R = T + P + N,$$

where:

R — ration in mg/day or cal/day,

T — expenditures for exchange, expressed in these units of measurement,

P — production,

N — unassimilated part of food.

This may be expressed by the value of food assimilability as follows: $R = U(T+P)$. However,

$$R = F \cdot \bar{C} \qquad (5)$$

In consequence of this

$$F = \frac{(T+P)\bar{C}}{U} \qquad (6)$$

Using this formula we obtain a filtration rate that must absolutely be maintained by Cladocera in order to secure adequate amounts of energy supplied with food, for covering the expenditures cn both exchange and increase.

The formula (6) illustrates that in this case the filtration rate depends upon

Gauld formula (F^1), food demand (F^2), and oxygen demand (F^3)

$\bar{C}$ mg of dry wt./l	$\frac{1}{U}$ %	U_q %	Filtration rate ml/ind. per day			R during experiment mg of dry wt. $\cdot 10^{-3}$/ /ind. per day	$\frac{R}{(T+P)U}$ %
			F^1	F^2	F^3		
0.06	80	1.5	10	86	11.2	0.6	18.5
2.0	40	10	7	42	40	14	24
0.05	80	1.5	133	550	150	6.75	30
0.15	50	2.0	2.6	9.2	3.0	0.38	30
6.0	20	10	0.30	0.30	0.30	1.8	100
0.2	80	1.5	23	27	26	4.6	100
0.2	80	1.5	14	18	15	2.8	100
0.2	80	1.5	26	25	24	5.2	100
0.2	80	1.5	10	22	22	2.0	40
2.2	30	6.5	4.8	5.3	5.0	10.6	100

the correlation between the food assimilability and its concentration. It results from this that the formula cannot be applied when F does not depend upon $\bar{C}$.

3. The filtration rate may also be calculated according to the above method concerning the demand for oxygen and the value U_q at a given food concentration.

Table III presents data on filtration rate, obtained for various representatives of Cladocera. It may be seen that when the food content was less than 0.2 mg of dry wt./l (this corresponding approximately to 0.1 cal/l, where Chlorella individuals serve as food), the filtration rate, observed during the examinations was adequate to satisfy the demand of Cladocera for oxygen, but did not satisfy their demand for energy. The demands for food were calculated using $K_2 = 0.33$. We may suppose that when food concentration is insufficient, K_2 should be of lower value. When, however, the food concentration ranges from 0.2 to 20 mg/l, and the examination is made correctly, all the values calculated must coincide. When food concentrations are considerably high, and where minimum and constant value F is noted, the so-called "surplus" feeding may be observed, provided that Cladocera do not have any special apparatus to remove the excess of food. The calculations of the value of rations at various concentrations, proved by the experimental studies of Sorokin (1966), demonstrate that within a determined limit the ration aims at an asymptote (Fig. 2), and may be calculated according to the formula $R = R_{max} (1-10^{-K\bar{C}})$. The example of such a calculation is given in Table III. However, if the filtration rate becomes constant, R increases again. We may expect that under these conditions $K_2 > 0.33$ (Table IV).

The value of both maximum and minimum filtration rates is related to the caloricity of food and to the possibility of food assimilation by the animals (Ivanova 1968). Figure 3 demonstrates that the higher is the assimilability of food, the lower is the concentration, at which the filtration rate begins to depend on the food concentration.

In addition, important is here also the problem of the relation between the food concentration and F/Q. The latter ratio is frequently used as an index of filtration effectiveness. It has already been noted that F/Q may range considerably (Jorgensen 1955, 1966).
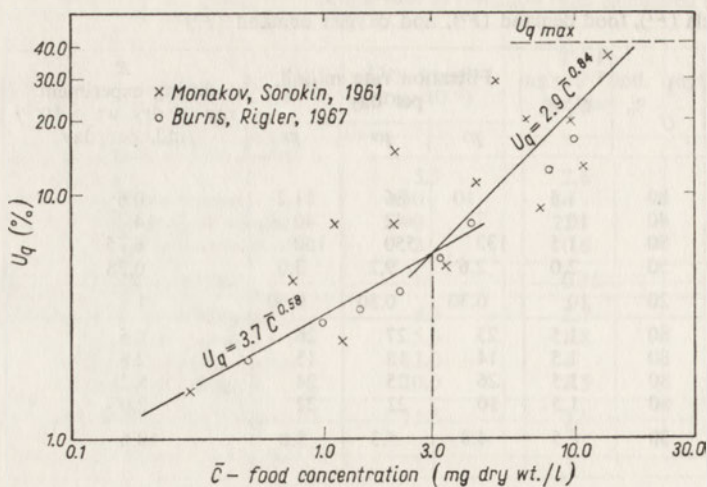
Fig. 2. Dependence of effectiveness in utilization of oxygen dissolved in water (U_q) upon mean food concentration ($\overline{C}$). Calculated according to MONAKOV and SOROKIN (1961), SUSHCHENYA (1958), SHUSHKINA and PECEN (1964), BURNS and RIGLER (1967), and RICHMAN (1958)

Table IV. Calculation of ration of Cladocera at various mean concentrations of algae. (Filtration rate calculated according to oxygen demand)

| Dry weight of crustaceans, mg	$\overline{C}$ mg/l	U_q %	F mg/day	R mg/day	$\frac{1}{U}$ %
0.001	0.2	1.7	2.55	0.510	98
	0.5	2.6	1.65	0.825	60
	1.0	3.8	1.13	1.130	44
	2.0	5.5	0.78	1.160	32
	4.0	8.5	0.51	2.200	22.6
	8.0	14.0	0.305	2.42	20.8
	10.0	18.0	0.240	2.40	20.8
	15.0	25.0	0.180	2.70	18.5
	20.0	30.0	0.142	2.84	17.5
	30.0	30.0	0.142	4.26	11.6
	40.0	30.0	0.142	5.68	8.8
0.010	0.5	2.6	11.5	5.75	59
	1.0	3.8	7.9	7.9	43
	2.0	5.5	5.45	10.9	31
	4.0	8.5	3.55	14.2	24
	8.0	14.0	2.15	17.2	19.8
	10.0	18.0	1.66	17.0	20.0
	15.0	25.0	1.18	17.6	18.2
	20.0	30.0	1.00	20.0	17.0
	30.0	30.0	1.00	30.0	11.0
	40.0	30.0	1.00	40.0	8.5
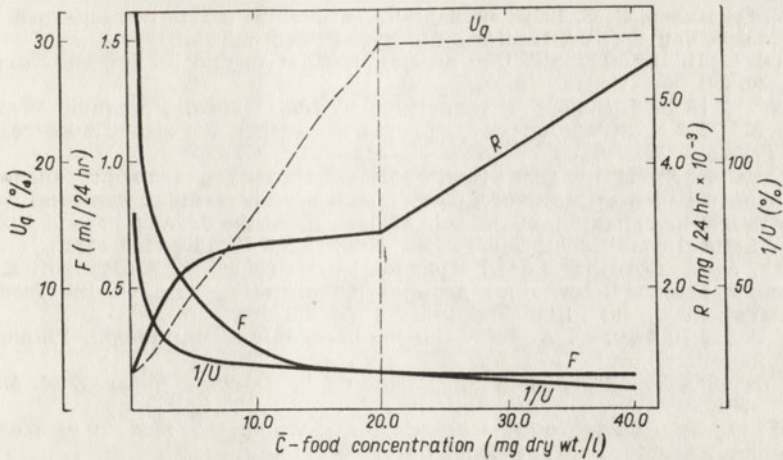
Fig. 3. Dependence of filtration rate (F), assimilability of food ($1/U$), and ration (R) upon mean food concentration ($\bar{C}$). Calculated for a crustacean 0.010 mg in weight (dry weight). 1 — filtration rate according to formula (3), 2 — food assimilability, 3 — ration

It results from (1) that

$$F/Q = \frac{1}{U_q M_{O_2}} \qquad (7)$$

If $35\% > U_q > 1\%$, and M_{O_2} is taken as equal to 7 mg/l, then the ratio F/Q ranges within the values of this index, i.e. 0.5 l and 14.3 l.

Taking into account (6) and a fact that

$$T = T_1 \cdot w^{0.81}; \quad Q = M \cdot w^{0.81}; \quad \text{and} \quad P = \frac{TK_2}{1-K_2}$$

we obtain:

$$F/Q = \frac{T_1 \cdot U}{M\bar{C}(1-K_2)} \qquad (8)$$

When $0.8 > \dfrac{1}{U} > 0.1$ and $30 > \bar{C} > 0.2$ mg/l, the calculated value F/Q is within the limits from 13.7 l to 0.66 l.

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Z. M. Gliwicz

CALCULATION OF FOOD RATION OF ZOOPLANKTON COMMUNITY AS AN EXAMPLE OF USING LABORATORY DATA FOR FIELD CONDITIONS

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ABSTRACT

On the basis of microscopic analysis of a plankton samples taken from the environment (the number of zooplankton, phytoplankton, bacterioplankton and tripton) as well as parameters obtained in laboratory conditions (the filtration rate characteristic for different species of zooplankton together with the type of food selectivity of these species) the food ration has been calculated for control zooplankton groups. This ration has been compared with the food rations of the same groups of zooplankton measured in an experiment in natural conditions.

There are serious difficulties in using the bioenergetic parameters, obtained in laboratories, to present the functioning scheme of the entire biocenosis or even its small fragment. First of all, it is difficult to obtain data for all dominant components of biocenosis, or only the trophic level or community, and what more it is not easy to estimate the error, while using the laboratory data for the complicated natural conditions.

Nevertheless such parameters are used e.g. when calculating the net production of entire communities, trophic levels or the intensity of their metabolism. It is more difficult, however, and is proved by those few analogous attempts in literature, to use these parameters in order to calculate consumption–food ration of the entire community i.e. to describe the quantitative phenomena, in which more than one trophic level takes part. This is the result of the usually complicated potential composition of natural food and also of the difficulties connected with the character of food selectivity of respective species.

On a quite simple example it was checked, whether the results of calculation of the food ration value of a natural community of consumers in natural conditions, on the basis of parameters obtained in laboratory conditions, are the same as the food ration value of the same community obtained by means of field experiment. The example used is the calculation of food ration value of the entire natural community of plankton primary consumers — community of filtrators and sedimentators — basing on parameters obtained in the laboratory for single species. For a community, for which the value of food ration

was obtained previously (GLIWICZ 1968) by means of field experiment, the parameters are as following (Fig. 1). First — filtration rate of five dominant crustacean species (after BELJACKAJA-POTAENKO 1964) and dominant rotifer species after ERMAN 1956) in the community we are interested in, and second — the character of food selectivity of these species.
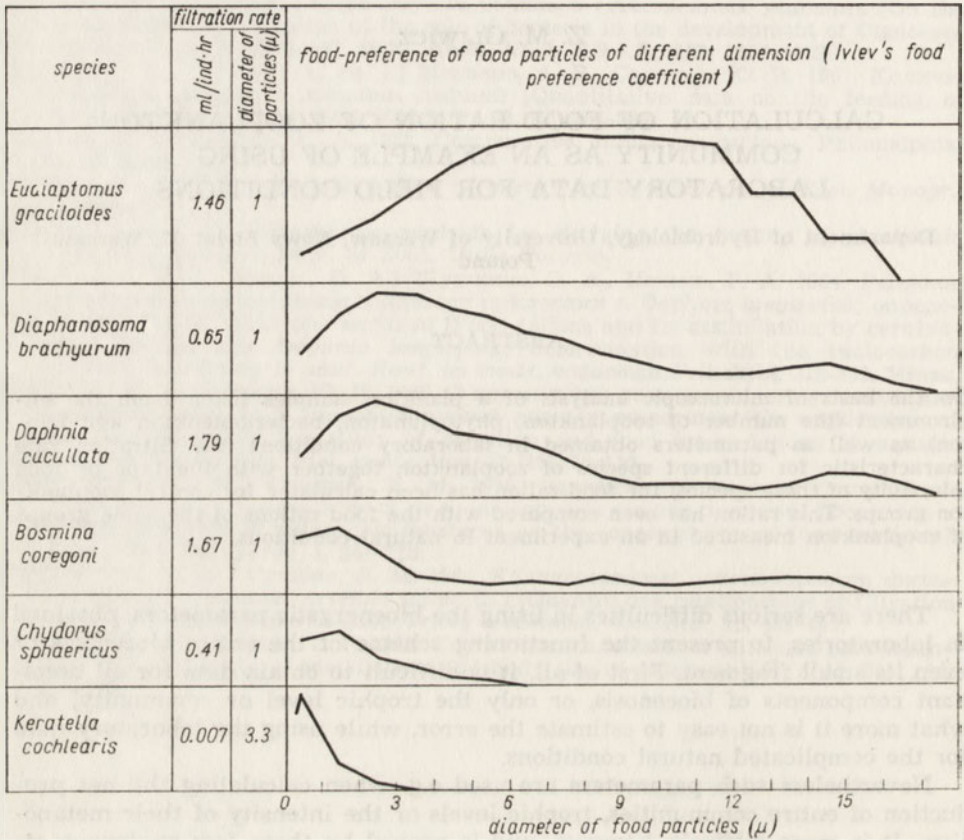
species	filtration rate		food-preference of food particles of different dimension (Ivlev's food preference coefficient)
	ml/[ind·hr	diameter of particles (µ)	
Eudiaptomus graciloides	1.46	1	
Diaphanosoma brachyurum	0.65	1	
Daphnia cucullata	1.79	1	
Bosmina coregoni	1.67	1	
Chydorus sphaericus	0.41	1	
Keratella cochlearis	0.007	3.3	

diameter of food particles (µ)

Fig. 1. Filtration of crustaceans — BELJACKAJA-POTAENKO 1964; filtration of Keratella — ERMAN 1956, food preference — GLIWICZ 1969

These data are from the experiment (GLIWICZ 1969), in which the mineral grains were given to crustaceans and rotifers, and the number of these grains was analysed in the environment and alimentary tracts. Each curve in Fig. 1 presents with the help of IVLEV's coefficient of food selectivity (1955) the differences in the filtrating intensity of food particles of various size by the given species. E.g. *Eudiaptomus graciloides* most intensively (most speedily) filtrates (consumes) food particles of the class of size between 5 and 10 µ of diameter, when e.g. *Daphnia cucullata* — from the class of size 2-4 µ of diameter. These curves prove that the particles of one size are more intensively (more quickly) filtrated and those of other size — less intensively (slowlier). This means that the filtration rate for a given size of particles — in this instance for bacteria

cells of an average diameter 1 μ or cells of *Chlorella* sp. of a diameter 3.3 μ — would not be the same in case of particles of a different size.

Having these laboratory data the procedure was as following: a plankton sample was taken from the environment of interest and the following information was obtained:

number of dominant zooplankton species,

number of small nannoplankton algae from various classes of size (net phytoplankton is of no interest here as it is practically not eaten by dcminant zooplankton species, as it results from a survey of literature on the subject (GLIWICZ 1969),

number of bacteria (total number of bacteria),

number of tripton particles from various classes of size, and average volumes of cells and particles belonging to various classes of size.

The first stage, when calculating the food ration of community, would be obtaining a curve illustrating the filtrating rate of food particles of various size out of the environment by the entire zooplankton community we are interested in. It is essential to assume that:

1) Coefficient of food selectivity for the given size of food particles is an indicator of intensity of consuming this size of particles by individuals of the given species.

2) This intensity may be presented in units of filtration rate. Filtration rate is the rate of filtering out (deprivation) of water the food particles and can be expressed in units of water volume per unit of time per one individual of the given species (e.g. in ml/ind./hr).

3. Filtration rate in dependence on the size of food particles is directly proportional to the consumption intensity of the given size of particles expressed by the coefficient of food selectivity. This does not sound paradoxical, if we have in mind the already presented definition of filtration rate. Filtration rate as the filtering rate of food particles out of water may be variable even then, when the rate of water flow through the filtration apparatus of animal does not change. That is, while filtering the water through the system of nets of the filter apparatus the food particles of various size are filtrated with different speed. The dependence of filtration rate on the size of food articles was already stated by McMAHON and RIGLER (1965). Also SUSHCHENYA (1959) stated the same thing with the help of IVLEV's coefficient of food selectivity.

Basing on these assumptions we assume after BELJACKAJA-POTAENKO (Fig. 1) that the rate of filtrating out of water of 1-μ particles by 1 individual of *Eudiaptomus graciloides* is 1.46 ml/hr. Having this number, we may lay off the scale of filtration rate on Y-axis, for the curve illustrating the character of food selectivity of *E. graciloides* (Fig. 1).

Let's turn to Fig. 2A where this curve is still marked by solid line. If 1 μ particles are filtrated with the speed 1.46 ml/hr, then e.g. particles of a diameter 3 μ shall be filtrated with the speed about 3 ml/hr (Fig. 2A). After taking into consideration the scale of filtration rate this curve — now marked by dotted line — presents the filtrating rate of food particles of various size by 1 individual of *E. graciloides* in ml/hr.

Let's use the same scale for a different species — e.g. *Daphnia cucullata*. This curve marked on Fig. 2B by solid line — also shifted from the previous figure (Fig. 1) — presents the differences in the filtrating intensity of food
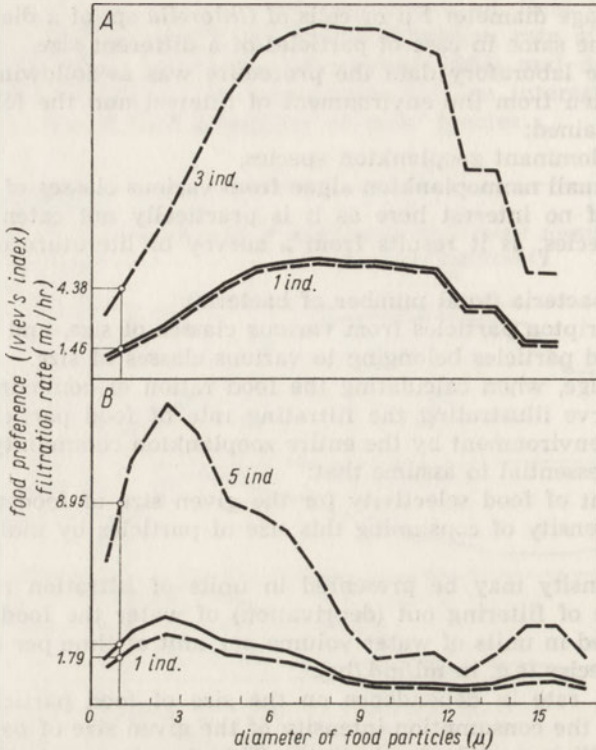
Fig. 2. Example of the conversion of the filtration intensity for a given species to the filtration intensity of food particles of different dimmensions (details in text). A — *Eudiaptomus gracioloides*, B — *Daphnia cucullata*. Solid line — food preference, dotted line — filtration rate

particles of various size by 1 individual of *Daphnia cucullata* in values of the coefficient of food selectivity.

Knowing already from the data of Beljackaja-Potaenko that the filtration rate of this species in the instance of particles of a 1 μ diameter is equal 1.79 ml/hr (Fig. 1), the curve point corresponding with 1 μ particles must be moved downwards in order to correspond with the value 1.79 on the scale of filtration rate taken into account on the Y-axis (Fig. 2B).

In order to know the filtrating rate of particles of other sizes all points of this curve have to be lowered in the same proportion. Thus the course of the curve remains unchanged, but this curve now marked by the dotted line denotes definite rational numerical values — the number of millilitres of food particles with various size filtrated within one hour. Thus we have a curve (Fig. 2B) illustrating the filtrating rate of food particles of various size from the environment by 1 individual of *Daphnia cucullata* in ml/hr.

Analogous curves are obtained for the remaining dominant species in the community we are interested in.

Then the values of each such curve are multiplied by the number of individuals of the given species in the volume of water interesting us e.g. 1 l of water. Let's say that in 1 l we have 5 individuals of *D. cucullata* then we

obtain a curve with values 5 times greater (Fig. 2B). Thus we obtain a curve illustrating the filtrating rate of food particles of various size by all individuals of *D. cucullata* from the volume of 1 litre.

The procedure with *E. graciloides* is analogous — let's say that we have in 1 l 3 individuals of this species (Fig. 2A) — and the same with other species. Now it is sufficient to add thus obtained curves (rather their adequate values) for all species, in order to obtain the curve presenting the filtrating rate of food particles of various size by all individuals of all dominant species out of the volume of 1 l, and so practically by the entire community in 1 l. Thus obtained curve (Fig. 3) provides information as to the rate, with which the
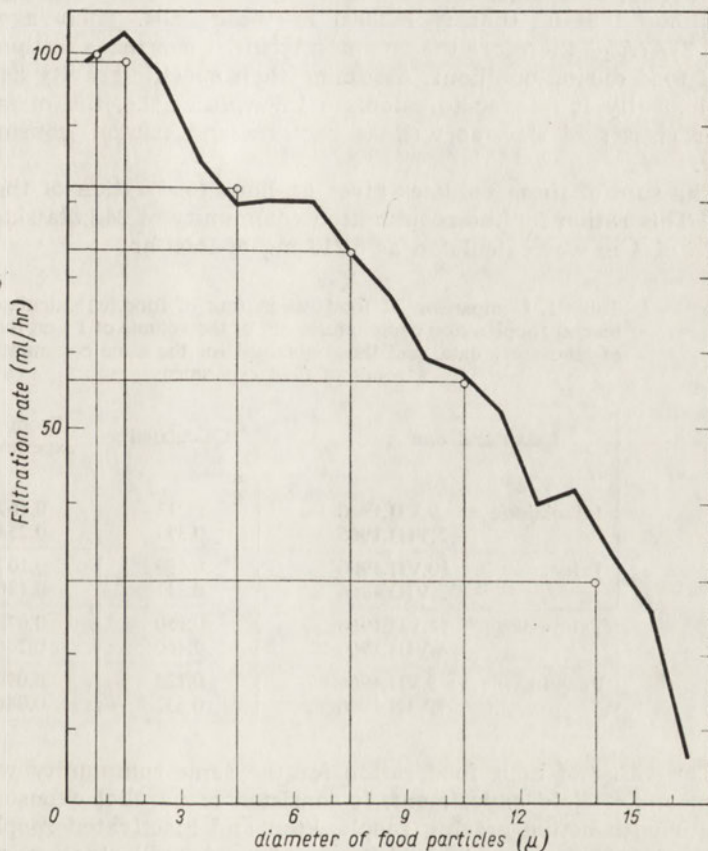
number of cells and particles in 1 ml	algae		2 243	1994	872	347	258
	tripton		19 518	454	392	383	356
	bacteria	5.1·10⁶					
volume of cells and particles		0.27	4.2	47.7	220.6	523.3	1 021.5

Fig. 3. Filtration rate of zooplankton community in 1 l and abundance of cells (algae and bacteria) and particular tripton of different size classes. Figures in the lower row indicate the mean volumes of cells and particles in μ^3

entire zooplankton community filtrates out of the environment algal cells and tripton particles from the class of size 3–6 μ of diameter (about 82 ml/hr), or bacteria cells having average measurements of volume 0.27 μ³ (about 100 ml/hr).

Having the field data — number of algal and bacterial cells and tripton particles from various classes of size (Fig. 3), that is the number of cells or particles in 1 ml, and their average volumes (Fig. 3), the food ration of the entire community can be calculated for of the volume of 1 l. E.g. filtrating rate of particles of the potential food from the class of size 3–6 μ of diameter by the entire community is (see Fig. 3) 82 ml/hr. As in 1 ml of water there are (Fig. 3) 1994 algal cells of the same class, the community filtrates during one hour 1994·82 that is 163,000 of these cells. Their average volume is (Fig. 3) 47.7 μ³ therefore the community in 1 l consumes in this form 7 millions μ³ of food during one hour. Assuming their specific gravity as 1 — about 7 μg. Analogically it is easy to calculate the volume, i.e. the mass of algae, from other classes of size, as well as bacteria and tripton, consumed during one hour.

The sum of these volumes gives an hour food ration of the entire community. This ration for the zooplankton community of Mikołajskie Lake from the depth of 4 m was calculated as 0.213 mg of food/hr.

Table I. Comparison of food ration (mg of food/hr) calculated for several zooplankton communities out of the volume of 1 l on the basis of laboratory data, and those obtained for the same communities as a result of field experiment

Lakes and date		Calculated	From the experiment
Mikołajskie	9.VII.1966	0.213	0.167
	2.VIII.1966	0.393	0.253
Tałty	10.VII.1966	0.189	0.107
	3.VIII.1966	0.211	0.186
Tałtowisko	11.VII.1966	0.150	0.078
	4.VIII.1966	0.460	0.206
Piłakno	5.VII.1966	0.128	0.094
	7.VIII.1966	0.532	0.086

The value of hour food ration for the same community was also obtained by means of field experiment. It consisted of parallel exposure of lake water in situ with active grazing zooplankton and inactivated zooplankton not taking food, and a comparison of the number of small algae, bacteria and tripton particles from various classes of size in both these variants after 4-hr exposure (detailed description of the method in the paper by GLIWICZ 1968). In this experiment the value of food ration of the same community was 0.167 mg of food/hr.

The value of food ration was obtained by means of calculation and also using the method of field experiment for communities from other lakes (Table I). It can be said that the calculated values and those obtained in the experiments are in the majority of cases quite similar, however these latter are sometimes several times smaller than the former (Table I). Of course these

differences can not be unmistakably explained as the sources of potential error are both in the calculation method and the method of experiment.

It may be expected that one of the most essential reasons for these differences is the age composition of populations of the dominant species — filtration rate assumed for the calculations was determined in the laboratory for mature individuals — yet in populations of dominant species in communities analysed here beside the mature forms were also younger individuals, which had a slightly lower filtration rate.

It seems, that while aiming at more precise information on the filtrating rate of particles of potential food of various size by the dominant species in communities we are interested in (and the dependence of this rate on such factors as temperature or food concentration) determination of the size of food ration of these communities in natural conditions basing on parameters obtained in laboratory conditions would be quite possible. It will be enough then to analyse the representative plankton samples (and temperature) for the given environment and period in order to calculate beside the net production of a zooplankton community also its consumption.

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SOME REMARKS ABOUT THE FOOD RATION

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ABSTRACT

The lecture contains remarks on the specific problems concerning the determina-
tion of the food ration in laboratory conditions for different animal groups as
well as a discussion concerning the ratio of the food ration to food assimilation.
Food assimilation is primarily dependent on quality of food (phytophagous animals,
predators and filtrators).

It has been assumed that food ration means the amount of food consumed
by an animal in a unit of time. The accepted unit of time is usually 24 hours
because of the 24-hr rhythm in the life of animals. This does not concern
animals that feed irregularly (e.g. leeches). In such instances other criteria
corresponding with the animal's behaviour have to be applied.

The consumed food ration is presented as the amount of individuals con-
sumed or as dry or fresh weight of food or as the per cent of consumer's body
weight or as per cent of its calorific value or in calories only. Calories or dry
body weight are the calculations providing the best information and the
easiest to apply in the energy balance. The latter value is more easily obtained
and in many instances completely sufficient as it allows further balance cal-
culations.

Food ration is one of the basic elements of energetic investigations. It de-
termines the amount of energy the organism is provided with.

As there are many systems of feeding of such animal groups as predators,
filtrators, phytophagous animals, the methods of determining the size of food
ration are various. Speaking in general three methods may be used: 1) labo-
ratory experiments, 2) field investigations together with the laboratory expe-
riment, 3) indirect methods of estimating the ration.

Because of the character of research work carried out in the Department of
Experimental Hydrobiology the greatest attention was paid on laboratory
experiments.

It is quite possible to determine the food ration in laboratory conditions
within the range of permissible error, but using thus obtained data for inves-
tigations of population in natural conditions is difficult and requires a great
deal of experience and critical judgement.

While preparing each experiment for determining the food ration one can-

not forget about the main factors having an influence on the rate of food consumption such as temperature, food accessibility, its different biological value, proportion between the size of consumer and prey.

There are two main approaches to determine the size of food ration in the laboratory. The first — investigations in conditions of food abundance, the second — in conditions imitating natural conditions. The difference lies only in the setting of the experiment. Further procedure is similar and closely dependent on the investigated object.

If the experiment is arranged in conditions of food abundance the principle is maximal limitation of food accessibility influence and creating the conditions of food abundance during the entire time of experiment. The amount of consumed food is most frequently obtained by estimating the food remains and subtracting this quantity from its initial amount. Depending on the object the amount of food is determined by counting and estimating the size — or weighing. In case of predators special attention should be paid to dead but not consumed or partly consumed preys.

Such situation frequently takes place, when the predator attacks equal or even bigger animal. Usually the animal is killed, but the predator is unable to eat it as a whole.

The next stage is determining the calorific value of consumed organisms, but measurements of calorific values of applied food made during the time of experiment are certainly of the greatest advantage.

Recently the isotopic method is becoming more frequently used. It is used, when investigating the food ration of filtrators, often of detritus insects and phytophagous animals, and sometimes even, when investigating predators. In some instances it is the only way possible to determine the food ration. This method is unquestionably more precise and also allows to determine the assimilated part. One should not forget that this method, however it seems simple, is in reality very complicated and requires a great deal of biological and physico-chemical knowledge.

Methods connecting field investigations and the laboratory experiments are various as for example: the method based on nitrogen balance (IVLEV 1939), DEMPSTER's protein method (1960), radioisotopes in natural conditions (ODUM and GOLLEY, CROSLEY), gravimetric method of PAINE (1965) and many others. I shall try to discuss briefly the most frequently applied methods based on analyses of alimentary tracts or the faeces contents.

Knowing the rate of food absorption from laboratory observations together with an analysis of alimentary tracts of animals caught in natural conditions, the size of food ration can be calculated. This method, however, seems to have several doubts. Preparation of alimentary tracts shows that usually preys are partly digested and their size and species, or at least the family, have to be reconstructed. This reconstruction provides us only with approximate values and the food ration should be estimated in calories or at least in dry weight of consumed food.

Apart from this, the method has other possibilities of making an error. While finding a determined remain of eaten organism, it is assumed that this organism has been entirely consumed. This assumption is very often wrong and may change the size of food ration even about one size of magnitude. Also the digestion rate and time of remaining in the alimentary tracts of various organisms are also important. Soft organisms are thoroughly digested and their

remains are less frequently found than the e.g. chitin remains. From the dissection we can find enough proof that the given organisms feed only with organisms having strong chitin covers. It also should be remembered that the time necessary for food to go through the alimentary tracts depends on the quantity and quality of consumed food, which is different in natural conditions and different in the experiment. It seems that this commonly applied method provides only with approximate data, which only together with data obtained in the experiment may give relatively true data on the size of food ration of a population of organisms in natural conditions.

On a similar principle the method of faeces analysis is based. This method was described by PAINE in 1965. The method determines the defecation rate during 24 hr in laboratory conditions, and then the hard parts of food are isolated from the faeces, identified and measured. After calculating that into the calorific value the size of ration is obtained. This method has the same errors as the method discussed above.

PHILLIPSON (1960) presents a very interesting method of determining the food ration in natural conditions based on estimating the dry weight and its calorific value. Knowing the assimilation, the size of food ration of animals in natural conditions may be relatively exactly determined. This method requires an assumption that the rate of emptying the alimentary canals in the field is the same as in the laboratory.

At the beginning of this paper a third method of determining the size of food ration was mentioned — the indirect method. Two examples of this method will be presented. First based on basic energetic equation as following:

$$C = P + R + F$$

where:

   C — food ration,
   R — production,
   P — respiration,
   F — faeces.

If we are in possession of data on the production, respiration and excretion — we may calculate the sum, which is the size of food ration.

The second example is the BLAXTER's method (1963) based on the condition coefficient. The condition coefficient is understood by BLAXTER as the proportion of mean dry weight to the average length of individual. He says that this coefficient is proportional to the size of food ration. BLAXTER determines several food rations in laboratory conditions, at the same time determining the condition coefficient of examined animals. Thus he obtained so to say "standardization curve", and then catching the animals in field and determining only their condition coefficient he read from this curve the size of food ration.

This method, however, gives some doubts. KAMLER (unpublished data) used this method on Plecoptera, but with a negative effect. On the other hand, it is known that some fishes during the spawning period have their best possible condition, but do not eat almost in that time.

As I have already mentioned at the beginning it is difficult to estimate the food ration precisely because of its mutability being of result from many factors such as temperature, animal's activity, quality and quantity of food, its accessibility and first of all the biological state of the organism, i.e. the size, age and egg production.

SARS (1903) gives the example of two Copepoda species of a similar weight

cultivated in identical conditions but only in different temperature (4.5° and 17°C). The species cultivated in lower temperature ate 19 μg of carbohydrates within 24 hr, while in the temperature 17°C — about 150 μg. In the latter case, the ration increased 8 times.

The size of food ration is also closely dependent both on the quality and quantity of food. If different kinds of plant food (FISCHER 1968) are given to a phytophagous fish (*Ctenopharyngodon idella*), then depending on the composition of given plants the food ration may range from 661 to 9786 cal. The food density also affects the size of food ration, but the opinions on the kind of that influence are divided. Investigations of MONAKOV and SOROKIN (1961) on *D. pulex* fed with Chlorococcales show that the size of food ration decreases together with the increase of the amount of food. KLEKOWSKI and SHUSHKINA (1966) obtained a similar result, investigating the predator *Macrocyclops albidus* fed with Paramecium. But RICHMAN (1958), basing on his experiments also on *D. pulex* fed with Chlamydomonas, says that the food ration increases together with the increasing density of food from 25,000 to 100,000 cells/ml/ /24 hr. According to RICHMAN the increase of food ration is more or less directly proportional to the increase of food density.

The physiological state of the examined organism is also a very important matter, which cannot be overlooked in the investigations. It can be accepted as a principle that young organisms have a greater food ration (measured as a per cent from the calorific value of body) than the older individuals. Several papers of IVLEV, KARZINKIN, WINBERG and others prove the same point. For example, KARZINKIN says that when the pike's weight changes from 0.13 to 1.37 g the ration decreases from 99.3 to 40.4%. WINBERG presents a table of the dependence between the increase of fish weight and decreasing food ration. This table shows that the fish weighing 0.01 g uses during 24hr the amount of food being of 56.3% of calorific value of its body, while a fish weighing 100 g — hardly 9.1%.

CUSHING (1964), in his paper about Calanus, insists on the significance of the interrelation of the food ration and the egg production. Calanus having a ration 5.307 mg of food per 24 hr produced on the average 23 eggs during 24 hr, but at the food ration 0.036 mg — scarcely 1.5 eggs on the average.

Determination of the food ration of investigated organism is an essential and indispensable matter to calculate its energy balance. However, for the organism itself the amount of assimilated food is more important than the amount of food consumed, i.e. the amount of energy the organism can dispose of.

Assimilation depends chiefly on the quality of food and the organism consuming this food. It can be accepted approximately (BLAXTER 1965) that proteins and fats are assimilated in 45–55%. This of course is not a rule as e.g. in some instances the fats may be assimilated even in 90%. Assimilation of carbohydrates is more difficult to generalize as e.g. cellulose is usually digested only in a small per cent, and in many instances is near 0. Still cellulose bacteria and some protozoan species have the ability to decompose cellulose. It has been accepted that higher organisms living with them in symbiosis assimilate cellulose in 53–70%. The other carbohydrates are assimilated in 60–75%. It rarely happens that the food assimilation is limited exclusively by the quality of consumed food. Tribolium may serve as an example, as there is a strain cultured on flour (with small addition of yeast) and its assimilation

is acc. to Klekowski et al. (1967) — 46%, what is of the same order as the assumed ability of amylum assimilation by animals (63%). Apart from the already mentioned factors, the assimilation depends also on all that discussed at the food ration. I shall only mention here the extremely controversial opinions on the subject of the effect of food density on the rate of assimilation.

Conover (1964) distinguishes two groups of animals, one having the assimilation above 60% and the other, less numerous group, where it is below 60%. His opinion is that assimilation does not depend on the amount of food. Klekowski and Shushkina (1966), Monakov and Sorokin (1961), Richman (1958) obtained different results. They say that at the increase of food density the assimilation decreases. Ivlev (1939), however, in his investigations on carp said that the food ration, depending on the season of year, fluctuates between 3.09 cal to 30.58 cal, at constant assimilation about 89%.

Speaking in general, the lowest assimilation is that of phytophagous animals and filtrators, i.e. these organisms, which feed with plant food having large content of carbohydrates, and or cellulose. Assimilation of *Ctenopharyngodon idella* (Fischer in press) cultivated only on plant food is about 13%, the assimilation of *Asellus aquaticus* about 26% (Prus in press). Discussing here the low assimilation of phytophagous animals the mammals such as sheep, rabbits, are not taken into consideration (in their case this value is about 60%). However, there are several opinions that these animals do not belong to phytophagous animals in the real meaning of this term, as they feed to some extent with meadow fauna. Also the above discussed symbionts decomposing cellulose should not be taken into account.

Assimilation of the filtrators is also low. According to Richman (1958), Monakov and Sorckin (1961) it is about 10–40% depending on the food density.

The assimilation of organisms having a very wide range of food selection (e.g. carp), is much greater and is about 80%. That of the typical active predators such as *Macrocyclops albidus*, pike, sturgeon, is high, about 80% (Karzinkin 1952, Klekowski and Shushkina 1966, Winberg 1956).

There is also a group of predators of low activity such as Actinia or some larvae of dragon-flies. The assimilation of these animals is smaller and is 52––68% in the case of Actinia (Ivleva 1964), and 35–46% in the case of the *Lestes sponsa* larvae (Fischer 1967).

In the end I would like to point out that in order to learn about some bioenergetic processes taking place in the organism, we cannot limit our investigations to determine the food ration or assimilation, but we have to know several parameters such as coefficients K_1 and K_2 of productivity, rate of production and age of organism. And after an analysis of these factors we can draw conclusions about the biological state of the investigated organism.

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CALORIFIC VALUE OF ANIMALS AS AN ELEMENT OF BIOENERGETICAL INVESTIGATIONS

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ABSTRACT

A survey is given of the literature data on calorific values in aquatic animals. The variation of this value (kcal/g dry weight) within each of several species amounted to 1–2 kcal and it was found to be dependent on such factors as developmental stage, physiological state, sex, season, and food conditions. High values are usually observed in these stages which precede the period of food shortage or that of diminished inflow of energy from the habitat, or still in these organisms which are ready for a conspicuous layout of energy in reproduction. The calorific values of body tissues of 63 species of aquatic animals vary from 4.2 to 6.8 kcal/g ash-free dry wt., with the majority of 37 species showing the range of 5.2–6.0 kcal and a mean value of 5.6 kcal/g ash-free dry wt. Basing on theoretical considerations of SLOBODKIN and RICHMAN (1961) which concern conceivable distributions of calorific value and their biological consequences, it was attempted to show in the material of 64 species belonging to 9 taxonomic phylla that the distribution of calorific values in aquatic animals approaches normal distribution. Biological consequences of this distribution are further discussed.

INTRODUCTION

Knowledge of calorific contents in biological materials is an indispensable element of bioenergetical studies on account of the necessity to express all parameters of energy processes in comparable units, i.e., calories.

In ecological literature, at least two concepts were generally accepted to describe calorific value of biological materials, namely, calories per gram of dry weight (cal/g dry wt.), and calories per gram ash-free dry weight, or calories per gram of organic matter (cal/g ash-free dry wt.); calories per gram live weight being the third useful concept.

There are several methods of calorimetry to assess calorific values which can be classified into two major categories: 1) direct calorimetry, 2) indirect calorimetry, the latter meaning assessment of calorific value from the incidence of chemical compounds of a known calorific content. These both categories of methods have positive and negative features, but the discussion of them as well as the accurracy of results are beyond the scope of this work. Concerning details on methods, reference should be made to original papers by IVLEV (1934, 1939), BŁAŻKA (1966 a,b), FISCHER (1967), PETINA (1966) — all on methods of wet combustion and chemical composition approach, to papers by RICHMAN (1958), SLOBODKIN and RICHMAN (1961), COMITA and SCHINDLER (1963), PAINE (1964, 1965) — all dealing with bomb calorimeters, as well as to papers on methods or those compiling materials

by McEvan and Anderson (1955), Paine (1964), Phillipson (1964), Górecki (1967), Prus (1968), Ostapenija et al. (1968), etc.

That calorific values obtained by means of different methods yield comparable results can be gathered, for instance, from Ivlev's paper (1934). This author reported on very similar pairs of values obtained by "wet" and dry combustions of Chironomidae, Gastropoda, Cladocera, and Gammaridae. Phillipson (1964), on the other hand, has obtained 6 differences out of seven examined to be non-significant when combusting the same materials in adiabatic type of bomb calorimeter (McEvan and Anderson 1955) and in non-adiabatic bomb calorimeter of his own construction (Phillipson 1964).

The accurracy of measurements (lack of summation of errors) and possibility of univocal estimation of variation which expressed as percentageous coefficient usually does not exceed over 1–2⁰/₀, are unquestionable merits of direct calorimetry, whereas the calculation of calorific value from chemical composition gives not only the total value of energy content in a given biological material, but also additional valuable data on the proportion of proteins, carbohydrates, and fats, from which one can also infer to some extent about the actual type of metabolism that follows in the animals examined. Unquestionable advantage of the non-adiabatic miniature bomb calorimeter is its precision of results and possibility to use it when the material at disposal is rather scarse (Phillipson 1964).

Two problems will be discussed now, namely, the variation in calorific value of animals' body within species, connected with the seasonal and developmental cycles, and interspecies variation of calorific value in aquatic animals.

INTRASPECIES VARIATION IN CALORIFIC VALUE

Despite of few data on this topic which are available at the present state of knowledge, it is obvious that calorific value of animals changes with their development. One should mention here papers by Richman (1958), Comita and Schindler (1963), Hmeleva (1967), Klekowski et al. (1967), Fischer (1967), and others. Most of the literature information is, however, fragmentary since it pertains to 2 or 3 developmental stages only.

Changes in calorific values of dry organic matter (ash-free) are connected with varying proportions of proteins, carbohydrates, and lipids, and those in total matter with all the above and with percentageous conteut of ash. Since total calorific values of proteins (5.65 kcal/g) and carbohydrates (4.10 kcal/g) are similar and rather low as compared to high energy values of lipids (9.45 kcal/g) (Hawk et al. 1954, after Richman 1958), the changes in total calorific value depend mainly on varying percentage of lipids in dry matter. Richman (1958), for instance, quoting Birge and Juday (1922) reported that percentage of lipids in reproducing *Daphnia pulex* with many embryos in brood pouches amounted to 21⁰/₀ dry weight, whereas in immatured individuals and in matured individuals with a few young in the pouch — it amounted to 3.9⁰/₀. In Richman's experiments on *Daphnia pulex*, the calorific value of the two size classes was similar (4.059 and 4.124 kcal/g dry wt.), and in the 3rd class, consisting of females with well-developed eggs or embryos it was higher by about 1 kcal and amounted to 5.075 kcal/g dry weight. Lack of a significant difference between 1st and 2nd class points to the fact that the calorific value per g dry weight in Cladocera is not correlated with the length of individuals, it is however correlated with their physiological state, i.e., reproducing period.

Comita and Schindler (1963) also pointed to the lack of dependence between the length of planktonic animals and their calorific value, exemplified by 3 Diaptomus species and *Calanus finmarchicus*. In the latter, the calorific

value of males 2.5 mm long ranged from 5.334 to 7.203 kcal/g ash-free dry weight. In females and V copepodites the highest calorific values were observed in individuals of an average length for a given size class.

Calorific value per unit weight seems to be correlated, on the other hand, with weight of planktonic crustaceans. Z. FISCHER (unpublished data) has found that both lipid content and calorific value per g dry wt. tend to increase proportionally with the increase in weight of individuals (Fig. 1).
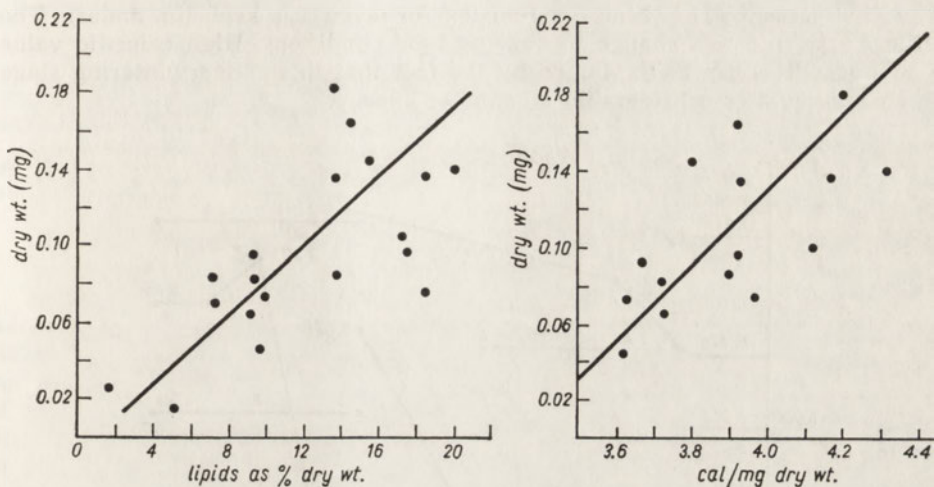

Fig. 1. Lipid content and calorific value in *Daphnia magna*. From FISCHER, unpublished

In dragonfly larvae of *Lestes sponsa* (Odonata), the calorific value changes within limits of 4.4–4.9 kcal/g, depending on weight of larvae, and thus on their age, since this finding is based on synchronized cultures run in the laboratory (FISCHER 1967). This dependence is not uniform though. The highest calorific values were found in larvae of 30 mg wet weight (Fig. 2).

Rather detailed information on changes in calorific value within a series of developmental stages of a species can be found in paper by COMITA and SCHINDLER (1963). This paper also includes data on seasonal changes in calo-
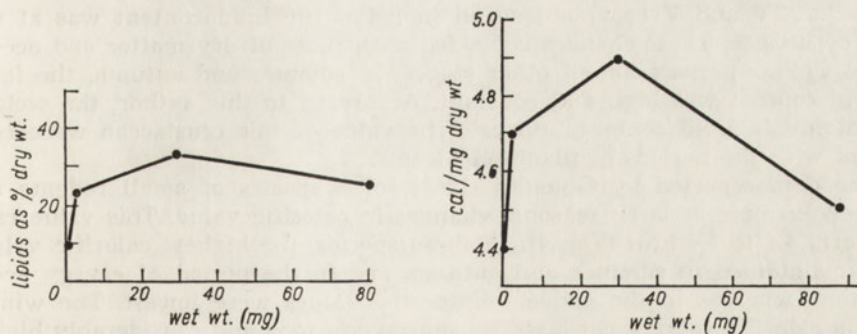

Fig. 2. Lipid content and calorific value in *Lestes sponsa*. From FISCHER 1967

rific value. Since the data on a marine crustacean, *Calanus finmarchicus*, were only described by these authors, they are transformed here to the graphical form (Fig. 3). Average oscillations within a year are considerable, from 5.9 to 7.4 kcal/g ash-free dry weight. The highest calorific value is that of individuals preceding maturity, that is V copepodite (7.416 kcal/g ash-free dry wt.) but calorific value of matured individuals is about 1 kcal lower (males) or even 1.5 kcal lower (females). Seasonal changes of calorific value are in this species very conspicuous. Sometimes, within one or two months, the calorific value increases by 1.5 kcal (in females) or even 2.0 kcal (in males). The authors attribute this change to varying food conditions. High calorific value in V copepodites can be explained by the fact that this is overwintering stage which accumulates considerable amount of energy.
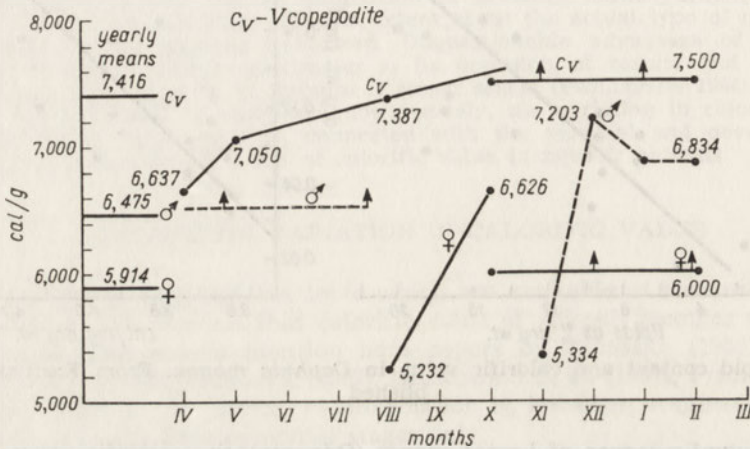

Fig. 3. Seasonal variation in ash-free calorific values of females, males and V copepodites of *Calanus finmarchicus*. Millport, Scotland, April 1962–March 1963. After COMITA and SCHINDLER 1963

Data by CONOVER (1968) speak in favour of high intraspecies variation, concerning the lipid content in 4 developmental stages of *Calanus hyperboreus* within a year cycle. The lipid content in females ranged from 14% of dry weight to over 50% dry weight, the latter value being maintained over a prepondering period of a year, i.e., from June to January, and in the remaining stages i.e., IV and V copepodites and in males the lipid content was at the level of 30–50%. These changes coincided with those of dry matter and occurred in similar periods for all other stages. In summer and autumn, the level of lipid content was high and constant. According to this author, the weight of individuals, lipid content, and calorific value of this crustacean were correlated with the periods of plankton blooms.

The data reported by GÓRECKI (1967) for 4 species of small rodents are another example of large seasonal changes in calorific value. This value ranged form 4.4 to 5.4 kcal (Fig. 4). In these species, the highest calorific values were maintained in summer and autumn, i.e., in the period of energy accumulation, whereas in the end of winter the values were lowest. The winter drop in calorific value was caused by shortage of food and considerably higher heat loss due to increased metabolism.

Fig. 4. Seasonal changes in energy values per gram dry weight of body of small rodents. A. f. — *Apodemus flavicollis*, A. a. — *Apodemus agrarius*, C. g. — *Clethrionomys glareolus*, M. a. — *Microtus arvalis*. From Górecki 1967
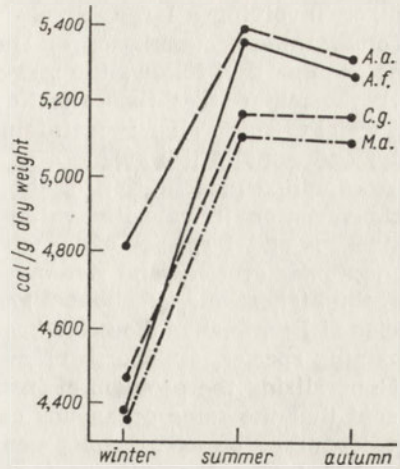
Relatively complete data on calorific value within the developmental cycle were collected for the flour beetle, *Tribolium castaneum* (Klekowski et al. 1967). The results of combustion in micro-bomb, gathering the whole developmental cycle which lasts about 30 days in this species, and includes the stage of an egg, six or seven larval stages, prepupa, pupa, and the period of adult life. The calorific value varies from 5.0 kcal/g dry weight in eggs to 6.7 kcal in the final larval stage and in prepupa. Thus the maximum of calorific value is usually observed in this stage which undergoes profound physiological
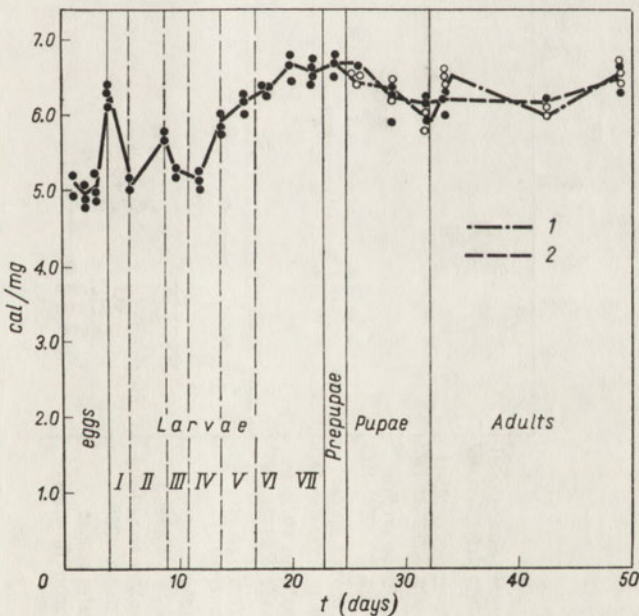

Fig. 5. Calorific value of 1 mg dry weight for developmental stages of *T. castaneum* — cI. 1 — males, 2 — females. From Klekowski et al. 1967

changes, involving a large expense of energy, connected with metamorphosis. A considerable accumulation of energy is also connected with a non-feeding stage of pupa that follows the stage of prepupa.

In the pupal stage the calorific value decreases down to about 6.0 kcal/g dry weight. This value is maintained in the adult beetles and is similar for males and females (Fig. 5).

A compiled presentation of the data discussed above shown in Fig. 6 reflects variation in calorific value of certain stages or sexes for 7 aquatic crustaceans and 1 species of insects. A relatively high calorific value of eggs of *Diaptomus arcticus* and *Artemia salina* as well as different range of variation, the highest one, of about 2 kcal in *Calanus finmarchicus*, low one in the species of Diaptomus (about 0.4 kcal/g) and average one (about 0.8–1.0) for the remaining species, are worth of mentioning.

Generalizing the problem of intraspecies variation of calorific value, it can be said that the same organisms can accumulate energy at a different quantity, depending on age, developmental stage, physiological stage, or food conditions. A high calorific value is usually observed in stages that precede the
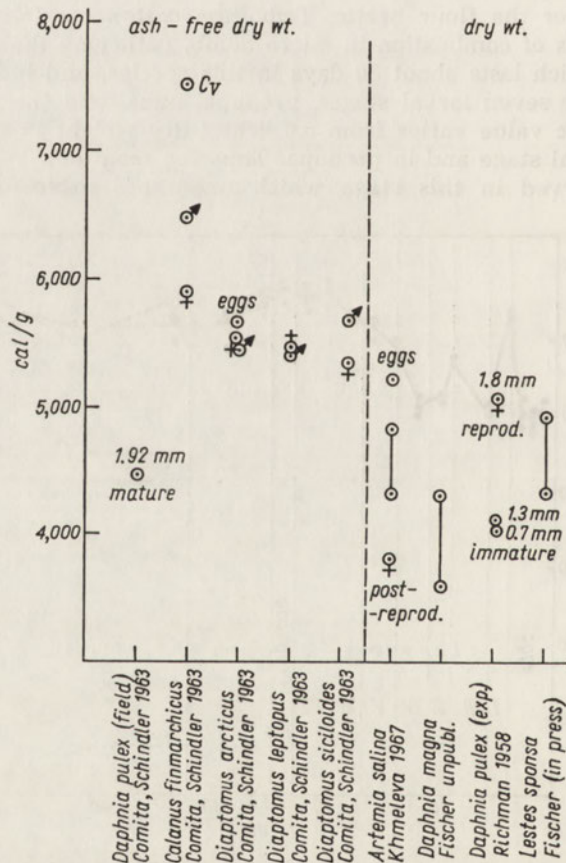
Fig. 6. Variation in calorific values in development of Crustacea and an insect

period of a complete or partial cessation of energy inflow, or in these organisms which are getting ready for a considerable loss of energy in the process of reproduction. The lack of energy entering an organism is connected either with physiological metamorphosis of an organism, or with unfavourable food conditions. The range of intraspecies variation is considerable one, usually around 1000 cal and in the case of *Calanus finmarchicus* it reaches even 2000 cal/g ash-free dry wt. (about 20 to 40% of the lowest calorific value).

INTERSPECIES DIFFERENCES IN CALORIFIC VALUE

At present the second type of variation in calorific value will be discussed, namely, the interspecies variation of this factor. One can ask a question which of the two values usually cited by various authors should be chosen for comparison. RICHMAN (1958) discussing KETCHUM and REDFIELD's (1949) data for Chlorophyceae suggests that calorific value of dry organic matter (ash-free value) is less suitable for such comparison since it has a higher variation due to varying ash content in the examined organisms. GOLLEY (1961), being of a contrary opinion, says that calorific value per gram ash-free dry weight reflects more precisely the difference between materials that are to be compared than does calories per gram dry weight, on account of various admixtures. Dealing with plant material such as roots or litter, it is difficult to wash out the soil particles which bring about underestimation of calorific content per gram dry weight.

It seems that when comparing calorific values between species or group of species one should rather depend on calorific value of organic matter since otherwise these are ash contents which are being compared and not the energy contents, or speaking more precisely, at least two sources of variation are involved, namely (1) variation in mineral contents, and (2) variation of energy content. This statement does not neglect, however, an important fact that when calculating general energy budgets the calorific value expressed in calories per gram dry weight is quite sufficient and more convenient than the other value.

OSTAPENIJA et al. (1968) have reported on a theoretically conceivable range of variation in calorific value of organic matter. According to these authors, this value can range from 4.0 kcal/g (80% carbohydrates and 20% proteins) to 8.3 kcal/g (70% lipids and 30% proteins). It is interesting to trace how this rather vast range is performed by nature. RICHMAN (1958), basing on KETCHUM and REDFIELD's (1949) data gives 6.154 kcal/g ash-free dry wt. as an average calorific value for 6 species of green algae. SLOBODKIN and RICHMAN (1961) when analysing calorific values of a number of animal species belonging to 5 taxonomic phylla reported that 12 of 17 species examined by them showed calorific value within the limits of 5.4–6.1 kcal/g ash-free dry weight. COMITA and SCHINDLER (1963), studying freshwater microcrustacea reported that calorific value ranged from 4.427 kcal/g in young forms to 6.675 kcal/g ash-free dry wt. in matured females. In marine species, *Calanus finmarchicus,* much higher values, 5.232–7.672 kcal/g ash-free dry wt. were observed.

PAINE (1964), describing his own results for Opistobranchiata gives range of 4.943–6.675 kcal/g dry weight.

OSTAPENIJA et al. (1968) reported that calorific value per gram of dry organic matter falls between 4.74–6.42 kcal, with 5.6 kcal being the most probable

value that can be encountered among animals. This conclusion was obtained from equation describing dependence of calorific value of dry weight and the per cent of organic matter content in dry weight. The equation for this dependence is as follows:

$$y = 0.0559x, \quad \text{with} \quad \delta y/x = 0.28 \text{ kcal/g},$$

where: y = calorific value of dry weight in kcal/g, x = % of organic matter in dry weight (see Fig. 7). According to OSTAPENIJA et al., this equation permits to calculate calorific value of dry weight of animal material from the percentage of organic matter, when per cent of ash content is known.
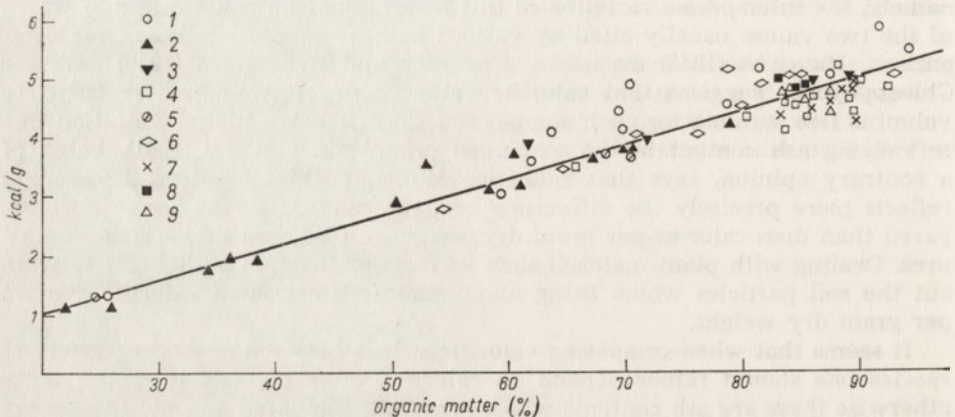

Fig. 7. Dependence of calorific value of aquatic organisms from organic matter content (%). From OSTAPENIJA et al. 1968. 1 — fresh-water plankton, 2 — plankton of Black Sea and Azov Sea, 3 — marine organisms, 4 — comparative data on Lamellibranchiata, 5 — *Gammarus marinus*, 6 — comparative data on crustaceans, 7 — *Mytilus galloprovincialis*, 8 — *Pachygrapsus marmoratus*, 9 — *Pecten ponticus*

Compilation of literature data accounted in this paper, involving 44 species of aquatic animals, to a greater extent different from those described by OSTAPENIJA et al. (1968) corroborates the finding on dependence between calorific value of dry weight of animal material and percentage of organic matter in this material (Fig. 8). The equation for the latter material is as follows:

$$y = 0.0557x,$$

where: y = calorific value of dry weight in kcal/g, x = % of organic matter in dry weight. Regression coefficient $b = 0.0557 \mp 0.0038$ (S.E.) is very similar to that reported by OSTAPENIJA et al. (1968).

TYPES OF FREQUENCY DISTRIBUTION OF CALORIFIC VALUES

SLOBODKIN and RICHMAN (1961) have presented three theoretical frequency distributions for calorific value of organic matter, discussing their biological and evolutionary consequencies. Among possible distributions they mentioned:
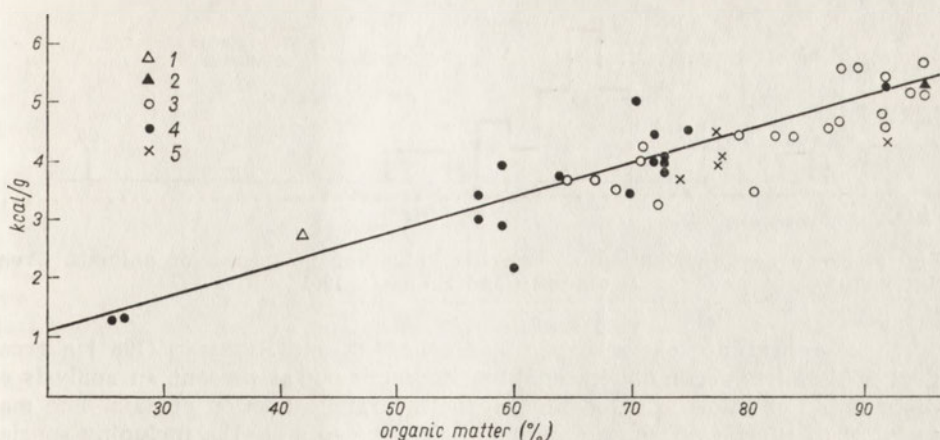1) Normal distribution (symetric), which can be expected from a number

Fig. 8. Dependence of calorific value of aquatic organisms from organic matter content (⁰/₀). 1 — Porifera; 2 — Annelida; 3 — Arthropoda; 4 — Mollusca; 5 — Chordata

of known, similar biochemical properties of animals with any deviation depending on small differences and errors in measurement of calorific value. This distribution suggests that there is optimum calorific value (cal/g) and deviations in both directions are being eliminated (SLOBODKIN and RICHMAN 1961).

2) Modal distribution, with peak of frequency shifted towards low values. This distribution would be expected, since natural selection always followed towards producing the highest number of progeny and only sporadically towards high calorific values. Biological consequence of this distribution would suggest that there is only one combination of organic compounds which result in a definite range of calorific values enabling survival of animals. These compounds are similar in all animals, however their combination resulting in low calorific value is not able to survive. Higher calorific value is expected to occur in these animals which temporarily accumulated much lipids, either due to a vast availability of food, or as preparation preceding the period of hunger or physiological stress (SLOBODKIN and RICHMAN 1961).

3) Multiple normal distribution (named by the present author). It is such distribution where there are large differences between taxonomic groups with normal distribution (symetric) within each group. Such distribution would have been expected from a premise that many features are common for one systematic category, and they differ between categories. Calorific value of organic matter would be one of such features. This distribution would indicate that calorific value is a secondary feature and a by-product of other selective factors. Such situation can be expected if and only if available energy has never been restricted in the period of organic evolution (SLOBODKIN and RICHMAN 1961).

Basing on 17 species belonging to 5 phylla these authors concluded that the second i.e., modal distribution can be observed in nature with its peak shifted to low values to a certain point beyond which there is no calorific values, and with a lengthening of the curve towards high calorific values (Fig. 9).
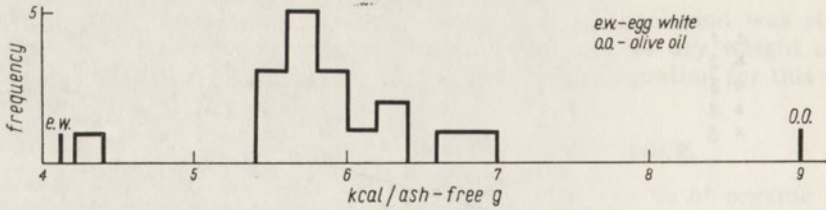
Fig. 9. Frequency distribution of calorific values of 17 species of animals. From SLOBODKIN and RICHMAN 1961

Since appearance of the paper by SLOBODKIN and RICHMAN (1961) a great deal of data has accumulated, enabling to carry out at present an analysis of distribution of calorific values, basing on a larger collection of data. The material of 64 species of aquatic animals belonging to 9 phylla, including species described by SLOBODKIN and RICHMAN (1961) points clearly to the first type of distribution, i.e., normal or symetric distribution (Fig. 10). The majority, that is 37 species reveal calorific value from 5.2 to 6.0 kcal/g ash-free dry weight. Medium value of this range is 5.6 kcal/g ash-free dry weight. This value was quoted by OSTAFENIJA et al. (1968) as most often found in animals.

The third type of distribution is not observed since after plotting names of taxonomic groups (orders or families) on a histogram of which the species marked with numerals are representatives show that the species belonging to the same taxonomic groups have calorific values scattered along the whole
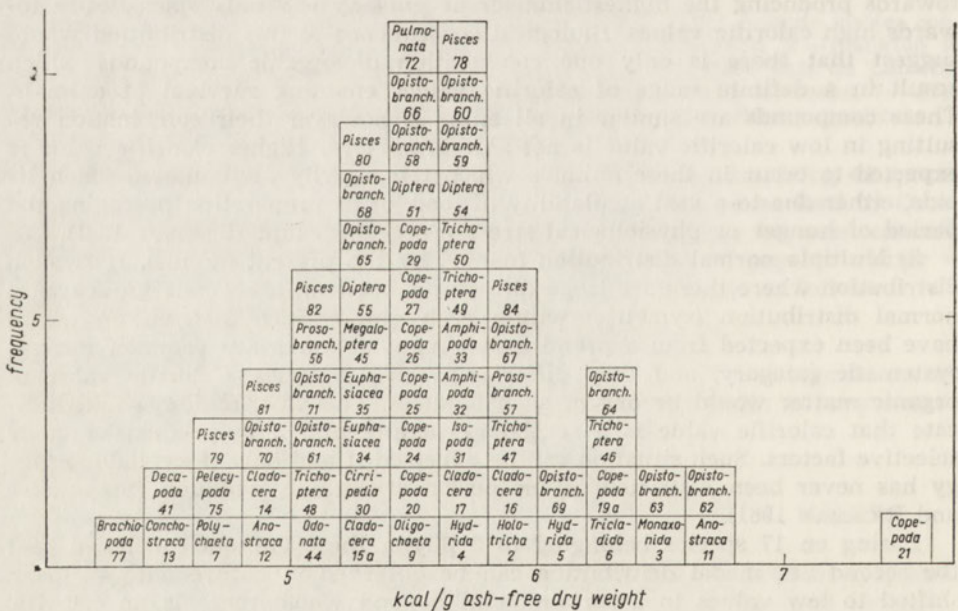

Fig. 10. Frequency distribution of calorific values of 64 species of aquatic animals. Numbers refer to position on the list of species in Table I

abscissa. Thus, for example, most numerously represented Opistobranchiata show low, intermediate, and high values. Only Copepoda reveal a very narrow range of calorific value (5.6 kcal/g ash-free dry wt.) with an exception of two species of marine crustaceans of Calanus.

Average calorific value of 1 g ash-free dry weight for the above described collection of species amounts to 5.528 kcal/g. If one assumes that the choice of species is random and that their frequency distribution is normal (which is evident from Fig. 10), 95% of all instances fall within the limits of $5.528 \mp$ ∓ 1.96 kcal, that is from 4.419 to 6.637 kcal/g ash-free dry weight. Standard deviation equals to 0.566 and includes the Sheppard's correction to the variance acc. to BAILEY (1959).

When constructing the histogram presented in Fig. 10, a condition was fulfilled that each species could be represented only by one value. When there were several independent calorific values obtained by different authors only one was chosen, the most reliable one, and in the case when there was a developmental series of data, the mean values for males and females or for different size classes were taken into account.
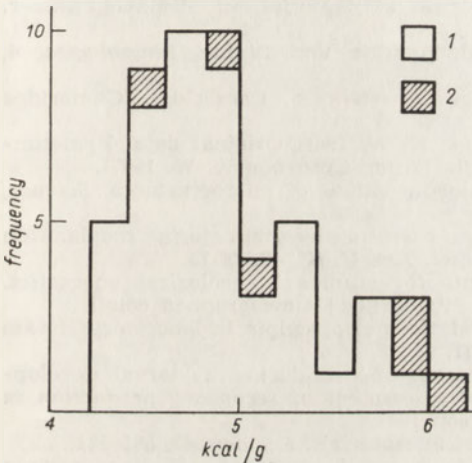

Fig. 11. Frequency distribution of calorific values of plant seeds of 51 species. After KENDEIGH and WEST 1965. 1 — whole, crushed and uncrushed, 2 — hulled

Normal distribution of frequency of calorific value was already suggested by PAINE (1965) by stating that after supplementing his data with those reported by SLOBODKIN and RICHMAN (1961) the distribution acquires more symetric form around value of 5.700 kcal/g ash-free dry weight.

In general, if one accepts biological interpretation given by SLOBODKIN and RICHMAN (1961) for normal distribution of calorific value which has been found among aquatic animals, it can be assumed that there is an optimum calorific value per gram dry organic matter, therefore, an optimum combination of proteins, carbohydrates, and lipids, but all deviations from this value, both in plus and minus, undergo selection. This assumption should be also supplemented with a preposition that each species reveals very high euroky in terms of calorific value, connected with actual life requirements, with physiology of development, food conditions, and fenology. This euroky ensures high chances of survival for this species and for its lasting in nature.

It is interesting to add, perhaps, that the modal distribution is found probably in terrestrial plants, when analysing calorific values of their seeds. The

diagram shown in Fig. 11, including 51 species is based on KENDEIGH and
WEST's (1965) data; thus for calorific values of dry matter, so that before
comparing it with the above discussed distribution for aquatic animals, it is
necessary to accept an assumption on rather constant ash content in seeds
of plants examined. If it were so, one can suppose that the second type of
distribution (modal distribution) can be found in such situation when each
deviation from the optimum value towards low values brings about a severe
selection (since it is selection of seeds, or disseminules), whereas deviation to
higher values is in this case neutral for survival. This hypothesis should be,
however, verified with an animal material, i.e., eggs, embryos, and neonates,
when an adequate number of data is accumulated.

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Table I. Index of species

No.	Phylum	Order of class	Species	Specification
1	Protozoa	Holotricha	*Paramecium caudatum*	—
2	,,	,,	*Tetrahymena pyriformis*	—
3	Porifera	Monaxonida	*Spongilla lacustris*	—
4	Coelenterata	Hydrida	*Chlorohydra viridissima*	—
5	,,	,,	*Hydra littoralis*	—
6	Platyhelminthes	Tricladida	*Dugesia tigrina*	—
7	Annelida	Polychaeta	*Strenelais articulata*	—
8	,,	Oligochaeta	*Limnodrilus* sp.	—
9	,,	,,	*Tubifex tubifex*	—
10	,,	Hirudinea	*Dina microstoma*	—
11	Arthropoda	Anostraca	*Artemia* sp.	naupli
12	,,	,,	*Streptocephalus seali*	10–15 mm, length
13	,,	Conchostraca	*Caenesteriella setosa*	4–7 mm, length
14	,,	Cladocera	*Daphnia magna*	—
14a	,,	,,	,, ,,	—
15	,,	,,	*Daphnia pulex*	—
15a	,,	,,	,, ,,	$\bar{x}$:0.7, 1.3, 1.8 mm
15b	,,	,,	,, ,,	—
15c	,,	,,	,, ,,	1.92 mm
16	,,	,,	*Leptodora hialina*	—
17	,,	,,	*Leptodora kindtii*	—
17a	,,	,,	,, ,,	—
18	,,	Copepoda	*Acartia clausi*	III copepodite
19	,,	,,	*Calanus finmarchicus*	$\bar{x}$ ♂ and ♀
19a	,,	,,	,, ,,	$\bar{x}$ 19 and 19b
19b	,,	,,	,, ,,	—
20	,,	,,	*Calanus helgolandicus*	—
21	,,	,,	*Calanus hyperboreus*	adult female
21a	,,	,,	*Calanus* sp.	—
22	,,	,,	*Cyclops furcifer*	IV copepodite
23	,,	,,	*Cyclops strenuus*	reprod. female
24	,,	,,	*Diaptomus arcticus*	$\bar{x}$ ♂ and ♀
25	,,	,,	*Diaptomus leptopus*	$\bar{x}$ ♂ and ♀
26	,,	,,	*Diaptomus siciloides*	$\bar{x}$ ♂ and ♀
27	,,	,,	*Mesocyclops edax*	adult female
28	,,	,,	*Simocephalus vetulus*	—
29	,,	,,	*Trigriopus californicus*	—
30	,,	Cirripedia	*Balanus cariosus*	without plates
31	,,	Isopoda	*Asellus aquaticus*	—
31a	,,	,,	,, ,,	lab. culture
32	,,	Amphipoda	*Carinogammarus Roeszli*	—
33	,,	,,	*Gammarus pulex*	—
34	,,	Euphasiacea	*Euphasia krohni*	—
35	,,	,,	*Meganyctiphanes norvegicus*	—
36	,,	Decapoda	*Uca pugnax*	$\bar{x}$:3 size classes
37	,,	,,	*Uca pugilator*	various size
38	,,	,,	*Secarna reticulatum*	,, ,,
39	,,	,,	*Panopius herbsti*	,, ,,
40	,,	,,	*Pridium limnosum*	small and large
41	,,	,,	*Cambarus robustus*	various size
42	,,	,,	*Cambarus immunis*	adults
43	,,	Ephemeroptera	*Stenonema pulchellum*	$\bar{x}$ lab. culture
44	,,	Odonata	*Lestes sponsa*	$\bar{x}$:4 age groups
45	,,	Megaloptera	*Nigronia serricornus*	—
46	,,	Trichoptera	*Hydropsyche slossqnae*	larvae

and their calorific values

Me-thod	No. samples	cal/g dry wt.	≠	cal/g ash-free dry wt.	≠	Ash %	References
C	1	3827	—	—	—	—	KLEKOWSKI and SHUSHKINA 1966
B	—	—	—	5938±207	2	—	SLOBODKIN and RICHMAN 1961
B	4	2719*	—	6475±111	1	58	PAINE 1965
B	—	—	—	5729±247	2	—	SLOBODKIN and RICHMAN 1961
B	—	—	—	6034±146	2	—	,, ,, ,,
B	—	—	—	6286±338	2	—	SLOBODKIN and RICHMAN 1961
—	—	—	—	4700	—	—	SLOBODKIN 1962 (after CUMMINS 1967)
B	6	5137±863	3	—	—	—	JENKINS 1959 (af er CUMMINS 1967)
C	—	5280	—	5547*	—	4.82	IVLEV 1939
B	1	5443	—	—	—	—	JENKINS 1959 (after CUMMINS 1967)
B	—	—	—	6737±863	2	—	SLOBODKIN and RICHMAN 1961
B	—	—	—	4932±184	1	—	COMITA and SCHINDLER 1963
B	—	3675*	—	4560±270	1	19.4	,, ,, ,, ,,
C	—	3694+	—	4988+	—	33.17	IVLEV 1934
C	22	3700	—	4967	—	—	FISCHER, unpublished
C	—	4365+	—	5674+	—	18.25	IVLEV 1934
B	—	4419	—	5362	—	—	RICHMAN 1958
—	—	—	—	—	—	17.6	BIRGE and JUDAY 1922 (after RICHMAN 1958)
B	—	—	—	4478±372	1	—	COMITA and SCHINDLER 1963
C	—	4239+	—	5926+	—	28.94	IVLEV 1934
B	—	—	—	5605±584	2	—	SLOBODKIN and RICHMAN 1961
B	1	5182	—	5434	—	4.6	COFFMAN et al. 1966 (after CUMMINS 1967)
C	—	5590	—	—	—	—	PETINA 1966
B	—	5531*	—	6194	—	—	COMITA and SCHINDLER 1963
—	—	5609*	—	6281	—	—	,, ,, ,, ,,
B	5	5687*	—	6369±130	1	10.7 m	PHILLIPSON 1964
B	—	—	—	5400±197	2	—	SLOBODKIN and RICHMAN 1961
B	—	—	—	7432	—	—	SLOBODKIN 1962 (after CUMMINS 1967)
C	—	5490	—	6210	—	11.6	PIETINA 1966
B	1	5330	—	—	—	—	WIERZBICKA 1967
B	1	4764	—	—	—	—	,, ,,
B	—	—	—	5547	—	—	COMITA and SCHINDLER 1963
B	—	—	—	5416	—	—	,, ,, ,, ,,
B	—	—	—	5488	—	—	,, ,, ,, ,,
B	—	—	—	5478±97	1	—	,, ,, ,, ,,
B	1	3798	—	—	—	—	KLEKOWSKI and IVANOVA in press
B	—	—	—	5515±277	2	—	SLOBODKIN and RICHMAN 1961
B	2	4596*	—	5283±38	2	13	PAINE 1964
C	—	3680+	—	5699+	—	35.52	IVLEV 1934
B	5	2957	—	4586	—	—	PRUS unpublished
C	—	4446+	—	5603+	—	20.66	IVLEV 1934
C	—	4035+	—	5695+	—	29.14	,, ,,
B	3	4810*	—	5251±131	1	8.4 m	PHILLIPSON 1964
B	5	4393*	—	5230±33	1	16.0 m	,, ,,
—	6	2514	—	—	—	—	CONNELL unpublished (after CUMMINS 1967)
—	2	2077	—	—	—	—	,, ,, ,, ,, ,,
—	2	2712	—	—	—	—	,, ,, ,, ,, ,,
—	2	1780	—	—	—	—	,, ,, ,, ,, ,,
—	2	1935	—	—	—	—	,, ,, ,, ,, ,,
B	6	3267±470	3	4502±623	3	27.6	COFFMAN et al. 1966 (after CUMMINS 1967)
B	1	3914	—	—	—	—	JENKINS 1959 (after CUMMINS 1967)
B	29	5596	—	—	—	—	TRAMA 1957 (after GOLLEY 1961)
C	—	4597	—	5008	—	8.2	FISCHER in press
B	2	5210±263	3	5375±253	3	5.9	COFFMAN et al. 1966 (after CUMMINS 1967)
B	2	5605±29	3	6375±842	3	11.7	,, ,, ,, ,, ,,

No.	Phylum	Order or class	Species	Specification
47	Arthropoda	Trichoptera	*Neophylax nacatus*	larvae
48	,,	,,	*Pycnopsyche antica*	,,
49	,,	,,	*Pycnopsyche lepido*	,,
50	,,	,,	*Pycnopsyche guttifer*	,,
51	,,	Diptera	*Simulium* sp.	,,
52	,,	,,	*Harnischia tenuicaudata*	,,
53	,,	,,	*Tanypus stellatus*	,,
54	,,	,,	*Chironomus gregarius*	,,
55	,,	,,	*Chironomus plumosus*	,,
55a	,,	,,	*Tendipes plumosus*	,,
56	Mollusca	Prosobranchiata	*Bithynia tentaculata*	—
57	,,	,,	*Thais lamellosa*	without shell
58	,,	Opistobranchiata	*Acanthodoris rhodoceras*	—
59	,,	,,	*Polycera atra*	—
60	,,	,,	*Triopha maculata*	—
61	,,	,,	*Dendrodoris albopunctata*	—
62	,,	,,	*Dirona picta*	—
63	,,	,,	*Hermissenda crassicornis*	—
64	,,	,,	*Bulla gouldiana*	without shell
65	,,	,,	*Hamionea virescens*	without shell
66	,,	,,	*Aglaja diomedea*	—
67	,,	,,	*Navanax inermis*	adults
67a	,,	,,	,, ,,	eggs
68	,,	,,	*Aegires albopunctatus*	—
69	,,	,,	*Hopkinsia rosacea*	—
70	,,	,,	*Flabellina iodinea*	—
71	,,	,,	*Limacina retroversa*	—
72	,,	Pulmonata	*Succinea ovalis*	without shell
73	,,	,,	*Modiolus* sp.	—
74	,,	,,	*Oxytrema silicula*	—
75	,,	Pelecypoda	*Sphaerium* sp.	—
75a	,,	,,	,, ,,	without shell
76	,,	,,	*Musculium* sp.	,, ,,
77	Brachiopoda	—	*Glottidia pyramidata*	
78	Chordata	Chondrichthyes	*Raja orinacea*	eggs
79	,,	Osteichthyes	*Ctenopharyngodon idella*	lab. culture
80	,,	,,	*Lepomis gibbosus*	—
81	,,	,,	*Lepomis macrochirus*	—
82	,,	,,	*Cottus bairdii*	—
83	,,	,,	*Cottus perplexus*	—
84	,,	,,	*Lebistes reticulatus*	—
84a	,,	,,	,, ,,	—

Notes:
B — bomb calorimetry.
C — calorific value obtained from chemical composition.
≠ Numbers following the columns with calorific values define statistical meaning of plus minus values in these collumns, namely 1 — standard deviation; 2 — 95% confidence limits; 3 — plus or minus the range.
      * The value has been made up from the remaining data supplied by the author or authors listed in the reference collumn.

Me-thod	No. samples	cal/g dry wt.	≠	cal/g ash-free dry wt.	≠	Ash %	References
B	3	5684±235	3	5982±390	3	4.9	COFFMAN et al. 1966 (after CUMMINS 1967)
B	6	3540±99	3	5196±912	3	31.2	,, ,, ,, ,,
B	—	—	—	5687±530	2	—	SLOBODKIN and RICHMAN 1961
B	1	—	—	5706	—	—	,, ,, ,, ,,
B	1	—	—	5521	—	—	DAVIS and WARREN 1965 (after CUMMINS 1967)
B	—	5344	—	—	—	—	TUBB and TORRIS 1965 (after CUMMINS 1967)
B	—	5607	—	—	—	—	,, ,, ,, ,,
C	—	5430+	—	5779+	—	8.04	IVLEV 1934
C	—	4686+	—	5372+	—	12.18	,, ,,
B	—	5844	—	—	—	—	TUBB and TORRIS 1965 (after CUMMINS 1967)
C	—	1359+	—	5186+	—	73.40	IVLEV 1934
B	4	5377*	—	5845±107	1	8.0	PAINE 1964
B	3	2963±157	1	5439±150	1	41	PAINE 1964, 1965
B	5	4088±254	1	5680±158	1	28	,, ,, ,,
B	6	4107±240	1	5641±153	1	27	,, ,, ,,
B	5	2189±157	1	5158±173	1	40	,, ,, ,,
B	3	3938±246	1	6675±241	1	41	,, ,, ,,
B	7	4497±191	1	6446±66	1	28	,, ,, ,,
B	4	4553±141	1	6352±99	1	25	,, ,, ,,
B	5	3909±129	1	5335±79	1	27	PAINE 1964, 1965
B	5	4083±43	1	5555±29	1	27	,, ,, ,,
B	5	3763±166	1	5992±77	1	36	,, ,, ,,
B	4	923±14	1	—	—	—	PAINE 1965
B	3	3023*	—	5309±216	1	43	PAINE 1964
B	1	3424*	—	6007	—	43	,, ,,
B	1	3460*	—	4943	—	30	,, ,,
B	5	3543*	—	5026±278	1	29.5m	PHILLIPSON 1964
B	—	—	—	5415±6	2	—	SLOBODKIN and RICHMAN 1961
—	3	4600	—	—	—	—	KUENZLER unpublished (after CUMMINS 1967)
B	—	910	—	—	—	—	DAVIS 1965 (after CUMMINS 1967)
C	—	1302+	—	4693+	—	74.40	IVLEV 1934
B	2	3423±819	3	4759±558	3	27.30	COFFMAN et al. 1966 (after CUMMINS 1967)
B	1	5219	—	—	—	—	JENKINS 1959 (after CUMMINS 1967)
B	—	—	—	4397±2140	—	—	SLOBODKIN and RICHMAN 1961
B	—	—	—	5600	—	—	SLOBODKIN 1962 (after CUMMINS 1967)
B	—	4338	—	4705	—	7.81	FISCHER, unplished
B	3	4066±47	3	5286±177	3	25.00	COFFMAN et al. 1966 (after CUMMINS 1967)
B	3	3719±32	3	4975±280	3	25.8	,, ,, ,, ,,
B	3	3952±81	3	5102±344	3	22.5	,, ,, ,, ,,
B	—	5287	—	—	—	—	DAVIS 1965 (after CUMMINS 1967)
B	1	—	—	5823	—	—	SLOBODKIN and RICHMAN 1961
—	—	4500	—	—	—	22.72*	PAINE 1965

+ The value has been calculated from chemical composition data given by IVLEV (1934), using calorific equivalents for carbohydrates, proteins, and lipids acc. to HAWK et al. 1954.

m The given ash content is a medium value of the range given by the author referred to.

x̄ An average, either given by the author mentioned in the list references, or calculated for him.

E. KAMLER

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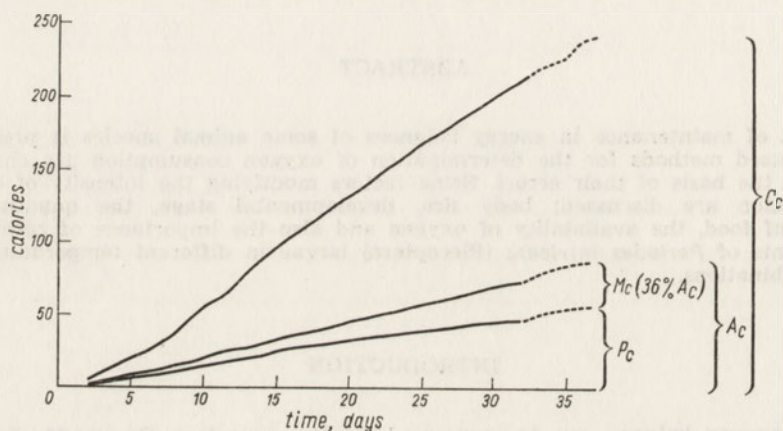
Fig. 1. Cumulative energy budget of an average larva of *Lestes sponsa* (adapted from FISCHER 1967). C_c — cumulated food intake, A_c — cumulated assimilation, M_c — cumulated cost of maintenance, P_c — cumulated production

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
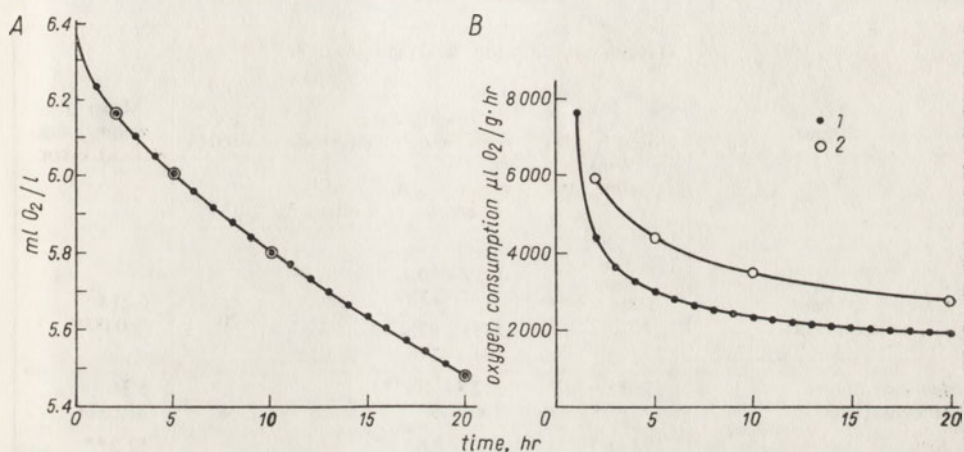
Fig. 2. Theoretical example of oxygen consumption measured by the closed-bottle method (from KAMLER 1969). A — changes in the oxygen concentration in the bottles containing animals: 1 — hourly electrode readings, 2 — WINKLER results (after 2, 5, 10 and 20 hours). B — oxygen consumption by animals: 1 — 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 expo-
sition 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 reali-
stic. 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 cur-
ves. KAMLER (1969) compared the respiratory rates of three freshwater spe-
cies, 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 $\mp$ std. error
	closed-bottles + Winkler (t=time, hr)	flowing-water respirometer+electrode			
		mean $\mp$ 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 Ctenopha-
ryngodon 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 Gastro-
poda species measured during 24hr in a flowing-water respirometer, oscil-
lated 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 indi-
vidual weighing less than 1.5 g of live weight has to be measured, the water
outflow from the respircmeter 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
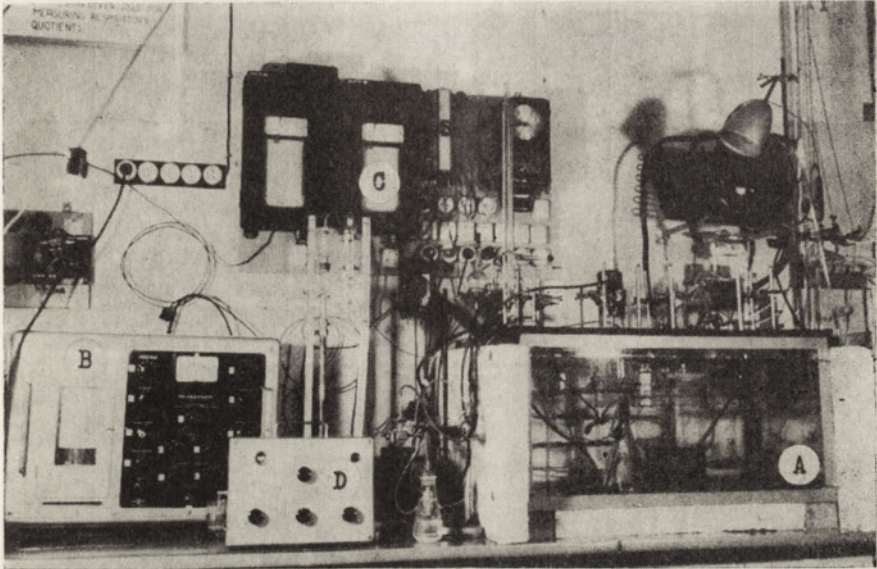
Fig. 3. General view of the flowing-water polarographic respirometer (from KLE-
KOWSKI and KAMLER 1968). A — constant temperature bath with reservoir-bottles,
respiration chamber and electrode chamber, B — polarograph, C — temperature
recorder, D — conductivity metre

in the water-bath (A). The water flow, the temperature and the level of oxy-
gen 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 (HEMMING-
SEN 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			live weight, mg	for period	Authors
	O_2 consumption $\mu l/\text{ind.} \cdot hr$ (W = live wt., mg)	temp. °C	O_2 consumption of 1 individ. weighing 1 mg converted to 20°C, $\mu l/hr$			
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 $\mu l\ O_2/ind.\cdot hr$, 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 $\mu l\ O_2/hr$) 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 $\mu l\ O_2/hr$) is much lower than in Tribolium and Ctenopharyngodon but fairly high in comparison with the remaining species. ISTENIC (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 $\mu l\ O_2/hr$ for one individual weighing 1 mg in $15°C$ or 1.231 $\mu l\ O_2/hr$ after conversion to $20°C$, which is close to that obtained by KAMLER (unpublished) for Perlodes, 1.600 $\mu l\ O_2/hr$. 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. ISTENIC (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 $cal\cdot 10^{-5}/ind.\cdot 24hr$, however, at density ratios of 3 : 1 and 1 : 1, the respiratory rate decreased to 13.4 and 8.06 $cal\cdot 10^{-5}/ind.\cdot 24hr$ respectively.
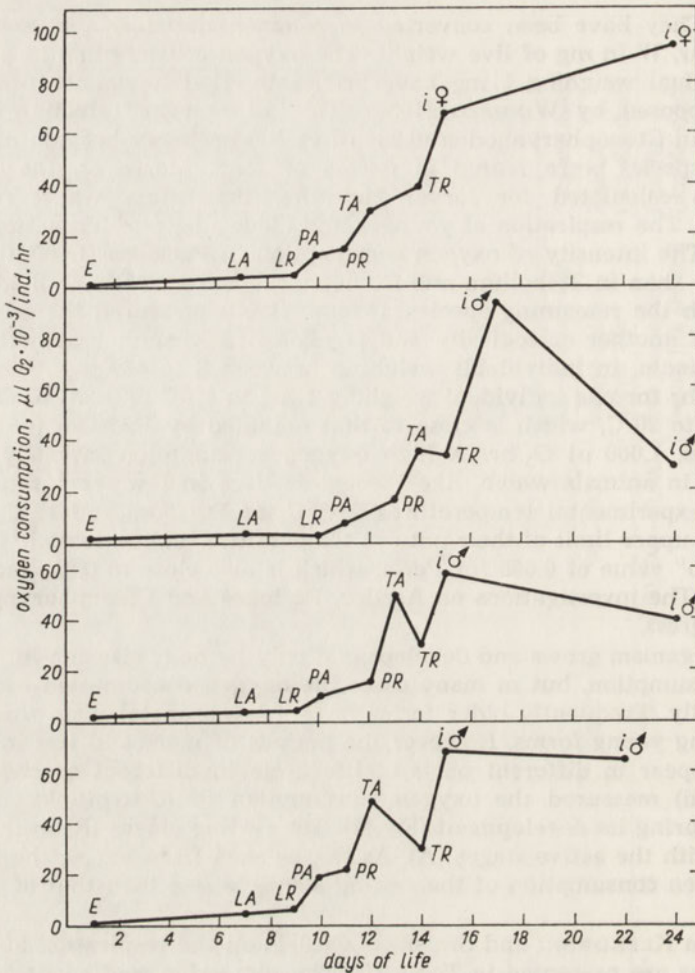
Fig. 4. Oxygen consumption of *Rhizoglyphus echinopus* during development (adapted from Stępień, unpublished). E — egg, L — larva, P — protonympha, T — tritonympha, I — imago, A — active stages, R — resting stages

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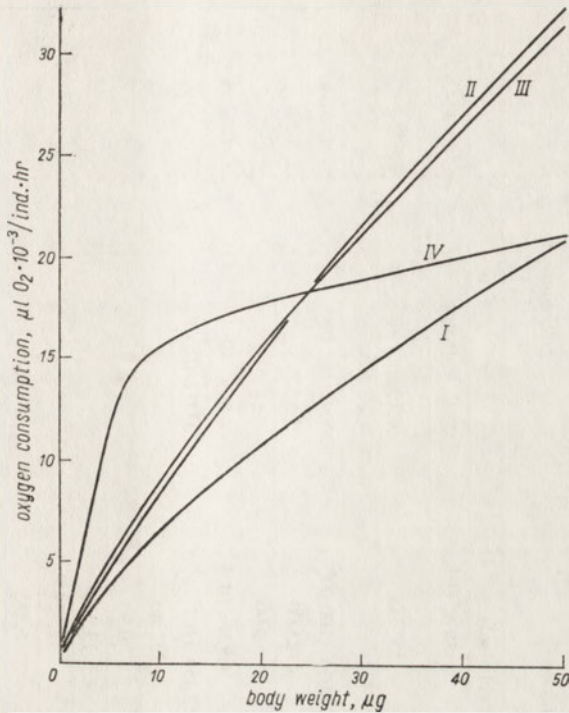
Fig. 5. Relationship between oxygen consumption and weight of *Macrocyclops albidus* in different food concentrations (from Klekowski and Shushkina 1966). I — 1000 ind./l, II — 10,000 ind./l, III — 50,000 ind./l, IV — 100,000 ind./l.

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 excretion, allows the quantitative estimation of the participation of metabolized carbohydrates, fats and proteins. Blażka (1966) showed that the participa-

Table IV. Three ways of estimation of metabolism

Determined	based on results of		*Ctenopharyngodon idella* (Pisces) Fischer (unpublished)		*Tribolium castaneum* (Coleoptera) 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/µlO_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. BLAŽKA 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,
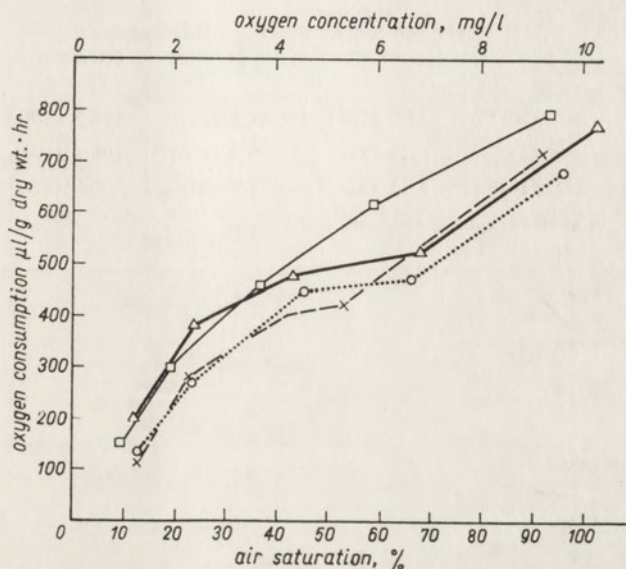
Fig. 6. Oxygen consumption of four *Anax imperator* larvae in relation to the oxygen content in water (from KLEKOWSKI and KAMLER 1968)

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.

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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.
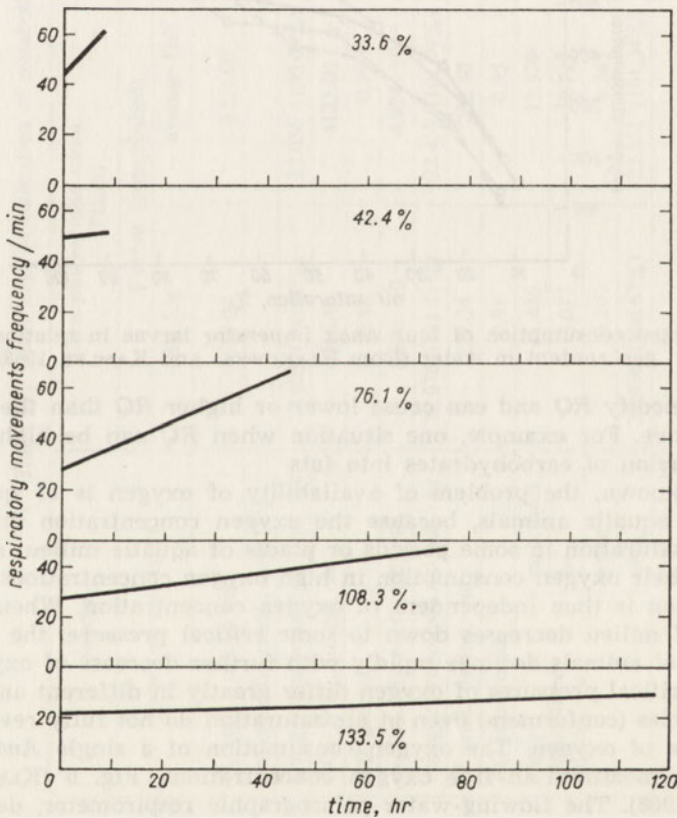
Fig. 7. Relationship between O_2 concentration and frequency of respiratory movements in *Perlodes intricata* larvae at 10.5°C (from KAMLER, unpublished). Per cent of air saturation at the start of experiment is indicated
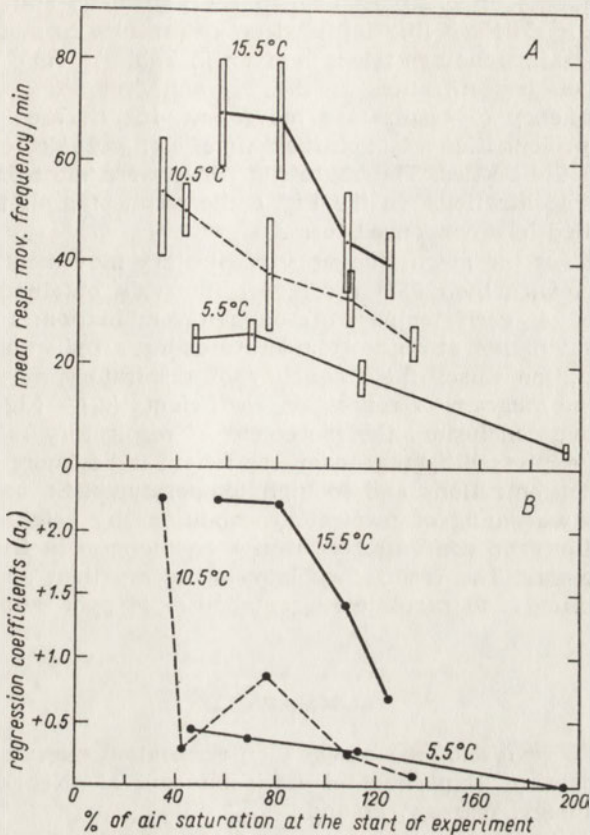
Fig. 8. Respiratory movement frequency in *Perlodes intricata* larvae in different combinations of oxygen and temperature (from KAMLER, unpublished). A — mean respiratory movement frequency/min. Vertical rectangles show 95% confidence interval, B — regression coefficients (a_1) of respiratory movements (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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PRODUCTION EFFICIENCY OF *PROCLADIUS CHOREUS* MG (CHIRONOMIDAE, DIPTERA) AND ITS DEPENDENCE ON THE TROPHIC CONDITIONS

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ABSTRACT

Studies have been carried out on the feeding intensity of a predatory benthic species — *Procladius choreus* — on other benthic organisms, and especially on Chironomidae and Crustacea. Experiments carried out in conditions close to natural ones showed that the food ration of *P. choreus* during 24 hr is about 10% of its body weight. The degree of food utilization for the growth was high — more than 60%. An increase of the number of easily accessible prey (*Chironomus* sp. larvae hatched from eggs) increased the predator's production and accelerated its development; the food ration within 24 hr increased 1.5 times and the degree of food utilization for the growth was similar as in series with natural concentration of invertebrates. Thus the negative effect of *P. choreus* on the number of other benthic organisms and especially on other Chironomidae larvae may be great in case of a supply to the habitat of young larvae developed from eggs, which are easily accessible to *P. choreus*. In case of a lack of Chironomidae larvae or their little accessibility to *P. choreus,* it feeds intensively on crustaceans. It seems that the number of this species may be often limited by food.

INTRODUCTION

Procladius choreus is a benthic predator often occurring numerously in various water habitats, and among others in the lake profundal (Stahl 1966, Giziński 1967, Kajak, Dusoge and Stańczykowska 1968 and others). The food of *Procladius choreus* consists mainly of small Chironomidae larvae, and crustaceans, other invertebrates being less frequently found in the alimentary canals of *Procladius choreus* (Belavskaja and Konstantinov 1956, Konstantinov 1958, 1961, Luferov 1956, 1958, 1961, Kajak and Pieczyński 1966, Izvekova 1967 and others). Young *Procladius choreus* larvae from the I instar feed on algae, while the larvae in the II instar feed mainly on animal food (Luferov 1958). The algae and especially diatoms are also found in the alimentary canals of larvae in the III and IV instar and this is accounted for the unfavourable trophic conditions (Luferov 1956), or it is assumed that the algae come from the alimentary canals of consumed non-predatory larvae (Belavskaja and Konstantinov 1956, Luferov 1958). Considering our observations and also Izvekova's data (1967) it can be said that the algae complete the animal food of older larvae and sometimes even to a great extent.

The aim of the work was to examine the feeding intensity of *Procladius choreus* and the degree of food utilization in different trophic conditions.

The material for the investigations was taken from the eutrophic, polymictic Lake Sniardwy, on the depth of 7 m. Chironomidae definitely dominated in the benthos of the lake (KAJAK and RYBAK 1966).

METHODS

Investigations were carried out with communities of organisms in sections of natural habitat, placed in the laboratory, in light and thermic conditions identical as those in the lake.

Experimental cylinders, 43 cm² of surface were used (KAJAK et al. 1965, KAJAK 1966), with the help of which sections of bottom with natural benthic association were taken without disturbing the structure of the sediment. Series of 8 cylinders were applied. One series was immediately sorted out after being
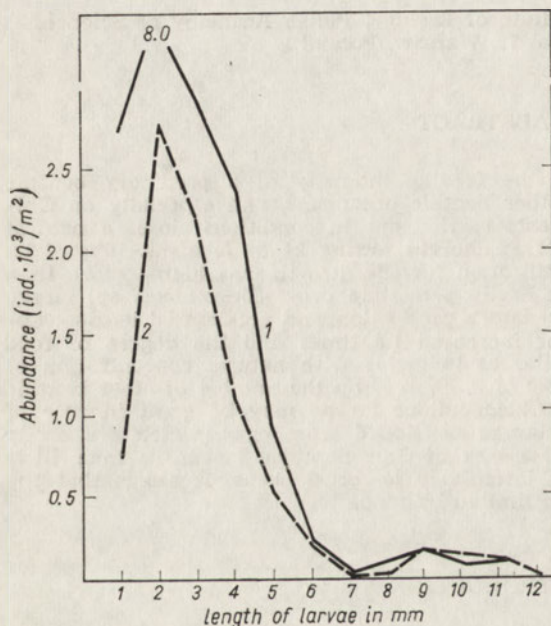
Fig. 1. Size structure of non-predatory Chironomidae. Series I. 1 — the state in the lake; 2 — after 7 days of the experiment

transported to the laboratory, and the remaining ones after incubation, which lasted 5-9 days. All samples were sorted out with the help of flotation method with sugar solution (KAJAK, DUSOGE and PREJS 1968), which allowed to estimate precisely the number of macrobenthos.

An analysis of the changes in number of Chironomidae larvae showed (Fig. 1) that *Procladius choreus* consumed small larvae not longer than 5 mm and therefore, when estimating the biomass of potential prey (non-predatory Chironomidae) only larvae not longer than 5 mm were taken into consideration.

Biomass (wet) of Chironomidae was calculated from the measured length of larvae using the formula $b = kl^3$, where b — biomass in mg, l — length of larvae in cm, k — experimentally calculated coefficient for various species

(Konstantinov 1958). The biomass losses of non-predatory larvae were determined from the differences between the initial state in the lake and the final one in the exposed cylinders, taking also into consideration the biomass increase of non-predatory larvae during the experiment.

According to Kajak and Rybak (1966) the average life time of larvae was accepted as 1 month (small species dominated: *Tanytarsus mancus, Cryptochironomus conjugens*) and their growth was calculated according to Konstantinov (1958).

The biomass increase of *Procladius choreus* was obtained from the difference between the initial state in the lake and the final one in cylinders. For the specimens of *Procladius choreus* which emerged during the experiment it has been assumed on the basis of own observations that their average size before pupating is 9.5 mm.

During the experiments, the emergence of non-predatory species was not observed.

The number of consumed crustaceans was determined on the basis of the proportion of crustaceans and Chironomidae remains found in the alimentary canals of the predator. The biomass of crustaceans was calculated assuming the average weight of an individual acc. to Stańczykowska and Przytocka-Jusiak (1968). Oligochaeta were not found in the food of *Procladius choreus*.

All calculations were made in units of wet mass assuming that the water ratios and calorific value were similar in case of food and consumer. Possible small deviations from this assumption should not change the results of the paper.

RESULTS

Field data (Table I) and laboratory data (Table II) show that the food composition of *Procladius choreus* may greatly differ depending on the accessibility and abundance of prey.

Table I. Seasonal feeding variation of *Procladius choreus*
in Lake Śniardwy

% Alimentary canals	Spring	Summer	Autumn
Empty[1]	32	18	3
With Chironomidae	2	48	14
With Crustacea	46	42	93

[1] with the exception of individuals containing only plant food.

Two first series of experiments (Table III) were carried out with a natural number of benthos. The basic food of *Procladius choreus* were small Chironomidae larvae and Crustacea.

During the experiment (7 days) the predator's biomass considerably increased (about 40%). The high degree of food utilization for the growth is remarkable.

Table II. Gut contents of *Procladius choreus* in various trophic conditions

		Mean number of Chironomidae in one alimentary canal	% of Procladius larvae containing in their alimentary canals	
			Chironomidae	Crustacea
Initial state	lake	1.0	58	86
Final state	control cylinders	1.0	67	33
	cylinders with an addition of eggs	6.2	100	11

In the III series the number of small *Chironomus* sp. larvae was increased by adding to the cylinders the egg-masses, out of which the larvae developed. A great abundance of easily accessible food led within the 9 days of experiment to a considerable increase of biomass (and even to pupating and emergence of *Procladius choreus*), and also caused a diminishing of the percentage of Crustacea in the alimentary canals of *Procladius choreus* (Table II).

The IV series similarily as the I and II was carried out with a natural benthic community, but the *Procladius choreus* larvae were younger. Total increase of the predator's biomass was similar as in series I and II, but high death rate of *Procladius choreus* (some 30%) was noticed. This might have been caused by a small number and smaller accessibility of prey for the small *Procladius choreus* larvae and by a decrease (as a result of feeding of non-predatory Chironomidae larvae — KAJAK and WARDA 1968, KAJAK 1968) of the amount of algae, which are a more essential food component for young *Procladius choreus* larvae than for the older ones.

Because of the mortality of *Procladius choreus* larvae and the impossibility to calculate the increase in biomass of dead larvae before they died, the numbers characterizing the increase of biomass of Procladius and food utilization for the growth in this series are lowered (Table III).

Increasing the number of predators (from 2.6 to 4.6 individuals in a cylinder, which corresponds to 605–1070 individuals per 1 m^2) caused a more intensive consumption of non-predatory Chironomidae and higher mortality of young *Procladius choreus* larvae.

The food consumption during 24hr is determined in relation to the predator's biomass. The recent data point to the fact that the food ration of *Procladius choreus* during 24hr may be even considerably greater than its weight (BELAVSKAJA and KONSTANTINOV 1956, KONSTANTINOV 1958, LUFEROV 1958). These results are a subject to some doubts, as they have been obtained in artificial conditions i.e. in cultures where the preys were considerably accessible. Meanwhile it is known that the composition and structure of the size of benthos components, spatial distribution and "organization" in the habitat have a great effect on the rate of prey consumption by predators (KAJAK and PIECZYŃSKI 1966). BELAVSKAJA and KONSTANTINOV (1956) found that an increase of the thickness of sediment layer at the same density per unit of surface of non-predatory Chironomidae and *Procladius choreus* caused much lower consumption. All, sometimes apparently small changes in the habitat or in the density of benthic organisms result in a strong reaction taking the

Table III. Dependence between the biomass production of *Procladius choreus* and its food base. Material from Lake Śniardwy. 5–9 day exposure of experimental cylinders. Vertical arrows show correspondingly the flying out or mortality of *Procladius choreus*

Series	Number ind./m²			Biomass in g/m²				Biomass increase of *Procladius choreus* in % (B)	Food utilization coefficient for the growth (A/B)	Food ration per 24hr in % of biomass of *Procladius choreus*
	Non-predatory Chironomidae < 5mm	*Procladius choreus* 1—3 mm	4 < mm	consumed animal food Chironomidae		Crustacea	increase of *Procladius choreus* in % (A)			
I	18,995	279	1465 · 1186		1.53 · 2.41		0.88	1.60	41.8	0.66	7
II	11,695	305	1256 · 951		1.19 · 1.76		0.57	1.19	37.8	0.67	7
III	135,000[1]	279	1465 ↑ · 1186		4.81 · 5.34		0.53	3.30	86.0	0.62	11
IV[2]	9,765	209	534 ↓ · 325		0.53 · 0.86		0.33	0.17	39.0	0.20	

[1] This number includes around 11,500 of *Chironomus* sp. larvae newly hatched.
[2] Because of the death rate of *Procladius choreus* larvae in series IV, numerical data are valid only for larvae, which survived, therefore these data are lower than in the remaining series where there was no mortality of *Procladius choreus*.

form of changes in number and condition of benthic organisms (KAJAK, DU-
SOGE and STAŃCZYKOWSKA 1968), and therefore their accessibility to the pre-
dator (KAJAK and WARDA 1968, KAJAK 1968). In this experiment, in series
with a natural community of preys and predators, in an undisturbed natural
habitat the food ration during 24hr was 7% of the biomass of *Procladius
choreus* (Table III). Taking into consideration the conditions of the experi-
ment — lack of a supply of potential preys: Chironomidae and Crustacea,
which could take place in the lake, and smaller density resulting from con-
sumption and also not taking into account the algae consumed by *Procladius
choreus* — the result obtained is probably lower than the real consumption
in nature. In the III series, where the number of preys was artificially in-
creased the food ration during 24hr was higher and covered 11% (Table III).
Even in this series, at the high accessibility of food, which resulted in the
high increase of the biomass and the emergence of Procladius, its food rations
were not much higher (especially when compared with the above cited very
high rations in the literature), and the index of the efficiency of using the
food for production did not change much either. However this is an average
for the whole 9-day period of the experiment, while the young *Chironomus*
sp. larvae were already consumed in the first days. The food ration per 24hr
would have to be higher at the beginning of the experiment.

It seems that the obtained values of food ration (of the order of 10%) and
the degree of food utilization for the growth (about 60%) are authoritative
for the analysed situations, however a periodical increase of the feeding in-
tensity is possible at the time, when the hatched young larvae appear. Food
rations of the same order (several %) were obtained when applying several
times greater number of *Procladius choreus* in relation to the natural one, in
previous experiments with sections of habitat with natural community of
organisms (KAJAK and PIECZYŃSKI 1966). IZVEKOVA (1967) obtained similar
low food rations in long lasting laboratory cultures at a full food accessibility.
High values of the coefficient of food utilization for the growth were found
for the predatory ones SOROKIN and PANOV 1966, PETIPA et al. 1967, CONO-
VER 1968, A. KAJAK and STEJGWIŁŁO-LAUDAŃSKA 1968, WELCH 1968), and in
certain forms in some periods of the life cycle (FISCHER 1967). It seems that
the high ratios of food utilization for the growth take place especially in si-
tuations, where there is a small food concentration (KLEKOWSKI and SHUSH-
KINA 1966). Probably this is what happens in case of benthic predators. Des-
pite of the sometimes great abundance of food its accessibility is low unlike
in laboratory conditions. This is among others supported by the already men-
tioned high increase of production and accelerated development of *Procladius
choreus* as a result of an increase of the abundance of easily accessible food.
It is also supported by the fact that crustaceans frequently dominate in the
food of *Procladius choreus* (Table II, TARWID 1969), despite the visible prefe-
rence cf Chironomidae larvae (Table III, LUFEROV 1958). These data seem to
point that the opinion about the great amounts of benthos consumed by *Pro-
cladius choreus* (BELAVSKAJA and KONSTANTINOV 1956, LUFEROV 1958) are
greatly exaggerated. However the influence of *Procladius choreus* on the
number of benthos may be quite big, as it causes among other things a strong
reduction cf the number of newly hatched and easily accessible larvae. In
situation of a significant increase of food accessibility — e.g. mass appearance
of young larvae, surely the food rations may be high in some periods.

CONCLUSIONS

1. Food composition of *Procladius choreus* shows a considerable quantitative and qualitative variation, depending on the food accessibility (Table I and II). Small Chironomidae larvae (Fig. 1) are preferred and the plant food is probably quite significant.

2. Food rations during 24hr, in conditions close to natural ones, did not exceed several per cent and were many times lower than at a greater food accessibility in laboratory conditions (perhaps they were slightly lower as the admixtures of plant food were not taken into account and the time of exposure was quite long.

3. Food utilization for the growth in conditions close to natural was very high — about 60% (Table III).

4. Addition of easily accessible food caused some increase of the ration per 24hr, great acceleration of the development and stimulation of the biomass production of *Procladius choreus,* while maintaining the high coefficient of food utilization for the growth (Table III).

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FEEDING AND PRODUCTION EFFICIENCY OF *CHAOBORUS FLAVICANS* MEIGEN (DIPTERA, CULICIDAE) LARVAE IN EUTROPHIC AND DYSTROPHIC LAKE

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ABSTRACT

Both consumption and selectivity of food by *Chaoborus flavicans* were studied during the experimental works conducted on natural plankton and benthos associations, under conditions approximate to natural. The method consisted in applying multiple increase in the number of Chaoborus and analysing losses in feeding organisms as compared with control experiment. It was ascertained that Chaoborus did not feed in benthos, whereas in plankton it consumed up to a dozen or so per cent of standing crop, and up to some scores per cent of production late in the summer stagnation.

In both lakes — eutrophic and dystrophic — Chaoborus consumed about one crustacean individual per hour. According to the unit biomass of crustaceans this gives considerable differences in its daily ration, i.e. several per cent of the Chaoborus weight in the eutrophic lake, and a dozen per cent or so of its weight — in the dystrophic lake. In consequence of this the production consumption ratio was also 1 : 2 (4.7% in the dystrophic lake, 8.8% — in the eutrophic lake), thus in both lakes it was low, probably due to a scarce growth of Chaoborus at that period. The period of the intense growth was here during the high production of zooplankton.

Larvae of the genus Chaoborus are an important constituent of fresh-water fauna, and an index element for strongly eutrophic and dystrophic lakes. Characterized by an active life, they mostly make daily wanderings (Berg 1937, Boruckij 1939, Northcote 1964, Stahl 1966) to spend the day mainly at the bottom, plunging even into soft deposits, the night, in turn, in water depths.

The larvae of the genus Chaoborus are predatory animals. It has been ascertained that at night, they eat up various components of pelagic zooplankton (Berg 1937, Comita and Munro 1960) and of zoobenthos (Jonasson 1965). Information on the feeding of the Chaoborus larvae is based, however, on the analysis of alimentary canals only. None of the investigators has examined both the selectivity and the quantity of the food consumed by the larvae, however. The analyses of the alimentary canals of the Chaoborus larvae, made for the purpose of this work (the larvae gathered on Sept. 8-9, 1967 in a lake during various day periods) have demonstrated that in the night hours about

10% of the total number of the individuals[1], sampled using plankton net, have had their alimentary canals filled in with food. In the day time, in turn, the number of the individuals (collected by means of bottom samplers) with the alimentary canals filled in with food was as follows: in the morning — 2.8%, at noon — 1.1%, in the evening — 0.9% (total number of the specimens analysed was 549). Most probably, these were individuals that did not still digest their food taken at night in the pelagial. The alimentary canals of the individuals caught in the day time in the pelagial were empty, too. These observations yield here only general data that allow us to illustrate the daily feeding cycle of the *Chaoborus flavicans* larvae.

To obtain data concerning both selectivity and amount of food taken by Chaoborus two kinds of experiments were carried out on September 1967 in two lakes: Mikołajskie Lake (eutrophic) and Flosek Lake (dystrophic).

a) Experiments concerning the consumption of benthos were carried out in the undisturbed portions of the environment with a complete, natural assemblage of benthos ("experimental cylinders method" — KAJAK et al. 1965, KAJAK 1966, 1968). The samples were transported to the laboratory and then kept during 48 hr at the same temperature as that in the lake. Examined were series characterized by 10 repetitions (5 in the dark, and 5 in the light), with 10 Chaoborus larvae added and with control series.

b) Experiments concerning the consumption of zooplankton. Water with natural assemblage of zooplankton was exposed in the plankton samplers (3 l in volume — Bernatowicz type, modified by GLIWICZ 1968) made of transparent organic glass. Beside 3 control instruments, each of the other 3 contained 10 individuals of *Chaoborus flavicans* (thus the density was here more or less eight times as much as that in the natural environment) placed in closed small boxes. These were opened automatically at the moment when the sampler was being closed. The exposition lasted 6 hr (18^{00}–24^{00}) in Lake Mikołajskie at a depth of 6 m, and in Lake Flosek — at a depth of 1.5 m, in the zone of a high numbers of the Chaoborus individuals at night.

After preserving in the formaline, the samples of both experiments were examined under the microscope (micro-benthos samples were examined using the technique applied by STAŃCZYKOWSKA 1966, plankton samples — in a plankton chamber).

During the experiments on benthos (frequency in Lake Mikołajskie amounting to 20,000 ind./m² of Copepoda, 900 ind./m² of Tubificidae and 100 ind./m² of Nematoda; the frequency in Lake Flosek — 1000 ind./m² of Copepoda, 100 ind./m² of Tubificidae, 100 ind./m² of Nematoda, and 600 ind./m² of Cladocera) no significant differences were noted in the numbers of potential Chaoborus food in the control series and those with Chaoborus larvae.

During the experiments on plankton, considerable losses in crustacean zooplankton were found (Table I). On the basis of these differences, the amount of zooplankton consumed by one individual of *Chaoborus flavicans* under natural conditions and natural density (0.4 ind./l) as well as the efficiency of Chaoborus production were calculated (Table II). The total number of the zooplankton crustaceans consumed by the population of *Chaoborus flavicans* at night (10-hour feeding was assumed) was in Lake Mikołajskie about 13%, in Lake Flosek — about 7% (Fig. 1).

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[1] Naturally, these numbers are only an index of consumption, since most specimens cast up their food during sampling, treatment with formalin, etc.

Table I. Effect of *Chaoborus flavicans* larvae on the numbers of natural plankton assemblages. Experiment in Lake Mikołajskie, 6-hr exposition (18^{00}—24^{00}), series of 3 instruments, each 3 litres in volume

Date	Variant of experiment	Density of Chaoborus individuals (ind./3 l)	Frequency of zooplankton in the final part of the experiment (ind./3 l)				No. of crustaceans eliminated by one individual of Chaoborus in 1 hr
			Copepoda		Clado-cera	Total number of plankton crustaceans	
			copepodi-tes and mature stages	nauplius-ses			
22.IX.1967	Control	1.2	50.5	22.0	4.9	77.4	0.88
	10 Chaoborus individuals added	11.2	19.6	2.6	2.3	24.5	
16.IX.1967	Control	1.2	5.9		128.6	134.5	0.81
	10 Chaoborus individuals added	11.2	1.6		84.2	85.9	

Table II. Food ration and growth efficiency of *Chaoborus flavicans* larvae late in the summer stagnation period in 1967

		Lake Mikołajskie	Lake Flosek
Daily increment (*P*) in mg		0.012	0.017
Daily food ration — *C*	in mg	0.138	0.365
	in % of body weight	3.6	12.5
P/*C* %		8.76	4.65
Average biomass of one *Chaoborus flavicans* larvae, in mg		3.8	3.2

The zooplankton of both lakes considerably differed, e.g. in Lake Flosek no nauplius forms of Copepoda were encountered; Cladocera visibly predominated. In Lake Mikołajskie Copepoda prevailed, mainly, however, as their postnauplial stages (Fig. 1).

In Lake Mikołajskie, a distinct preference in consumption of Copepoda naupliuses was ascertained (note their high frequency in the assemblage). In Lake Flosek, in turn, this concerns the postnauplial stages of Copepoda, irrespective of their low frequency (Fig. 1).

On the basis of the results obtained the daily food ration of the *Chaoborus flavicans* larvae at the latter part of summer stagnation was calculated (Table II). As compared with the zooplankton production, (that in August of various years was 4.4 and 2.5 mg/l — HILLBRICHT-ILKOWSKA and WĘGLEŃSKA 1970, i.e. 3.5 mg/l on an average), the population of the Chaoborus larvae consumed about some scores per cent. Of course, this is an orientation value
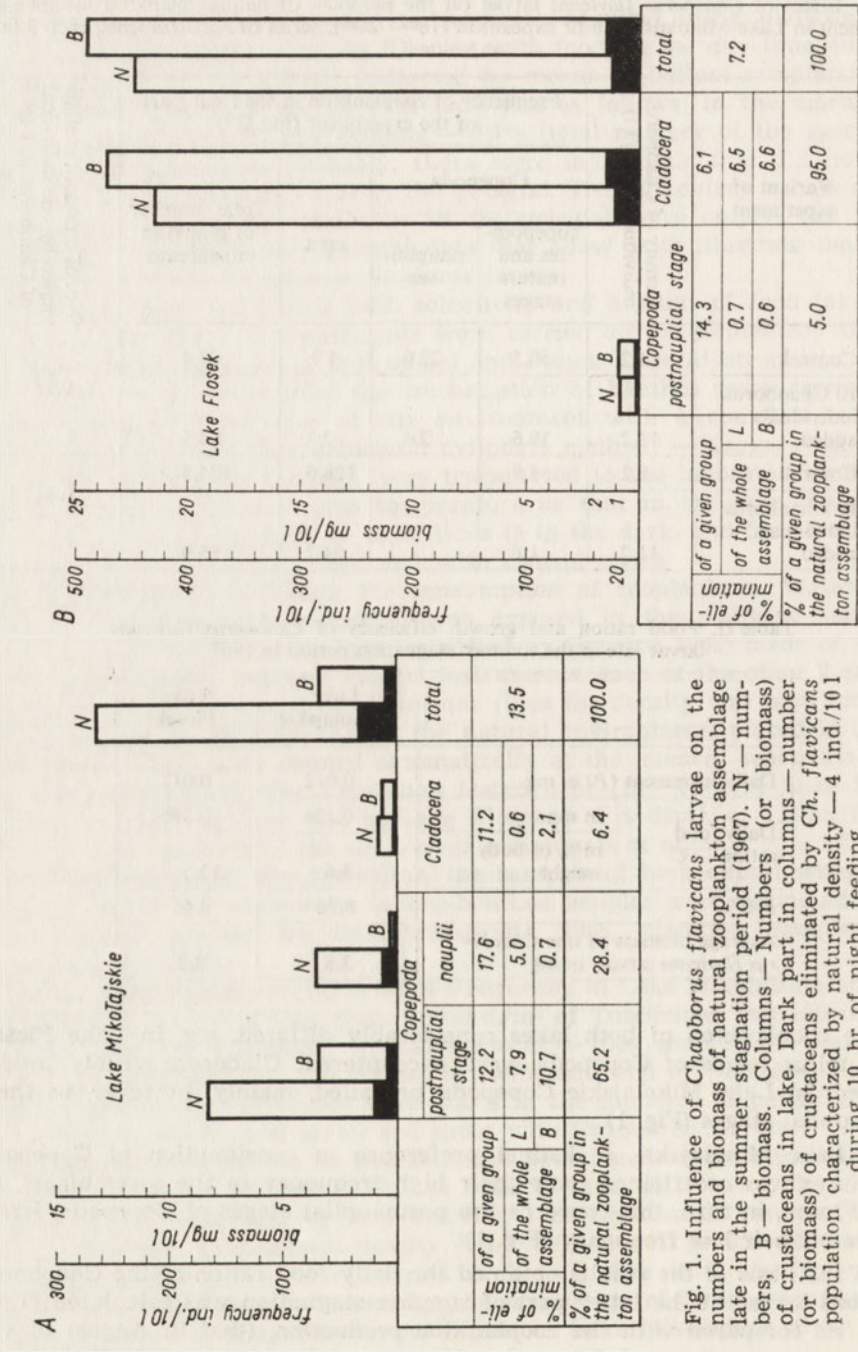
Fig. 1. Influence of *Chaoborus flavicans* larvae on the numbers and biomass of natural zooplankton assemblage late in the summer stagnation period (1967). N — numbers, B — biomass. Columns — Numbers (or biomass) of crustaceans in lake. Dark part in columns — number (or biomass) of crustaceans eliminated by *Ch. flavicans* population characterized by natural density — 4 ind./10 l during 10 hr of night feeding

only. To obtain more precise data we have to take into account the differentiation in vertical distribution of zooplankton, the feeding intensity of the Chaoborus larvae under conditions of various food concentration and at various times of night feeding, etc. A question arises, however, whether the food rations, calculated on the basis of the method described above, are completely authoritative. Some doubts may be a result of: 1 — eightfold density of predators during the experiment, as compared with the natural density and considerable losses in zooplankton during the exposition, particularly in Lake Mikołajskie (Table I); and 2 — considerably higher food ration of Chaoborus in Lake Flosek, where the food concentration was higher than that in Lake Mikołajskie. However, the following are contrarguments brought here to mind:

ad 1. The number of the crustaceans consumed was in both lakes similar, apart from the considerable differences in their concentration. One Chaoborus larva ate up during the experiment about 5 crustacean individuals. The differences in food ration were not a result of the food concentration, but of the size and unit biomass of the preys consumed (naupliuses in Lake Mikołajskie and Cladocera in Lake Flosek). This result suggests that even the low amounts of food — a consequence of feeding activity of Chaoborus — did not limit the value of its food ration. Most probably, decisive was here the quality of food (the size of the individuals caught) that did not change during the experiment.

ad 2. The data presented by HILLBRICHT-ILKOWSKA and KARABIN (1970) demonstrate that various concentrations (from natural to increased several times) of *Leptodora kindtii*, a predator with the character and feeding intensity resembling those of Chaoborus, were responsible for only insignificant differences in its food ration.

These facts prove the authoritativeness of the values of food ration considered, and of the coefficient of production efficiency, as well as that of fairly considerable change in these values, depending upon the actual food situation.

The examinations of feeding of the *Chaoborus flavicans* larvae were made at a period of slow growth of the larvae and of small daily increments (Fig. 1). The daily increment (P) of the larvae during the period of the experiments amounted to 0.012 g in Lake Mikołajskie, and 0.017 g in Lake Flosek. Probably, in the period of a rapid growth and, proportionally, considerable daily increments, the food consumption by the larvae is more intense.

The individual growth of the Chaoborus larvae shows a positive correlation with the production of the crustacean plankton. The high daily increments in biomass of Chaoborus take place during the high production of zooplankton. Later both the biomass increment of Chaoborus and the zooplankton production diminish (Fig. 2). The period of the intense growth of the Chaoborus larvae is considerably short, as compared with a long, annual life cycle, and amounts barely to 30 days (Fig. 2).

Accepting tentatively (according to BERG et al. 1962, and BERG and JONASSON 1965) that the respiration of one individual of Chaoborus is equal to 0.4 microlitre O_2/hour we may calculate that during 10 hr of night feeding, it makes in Lake Mikołajskie approximately 25%, and in Lake Flosek — hardly 9% of the day ration. It is, however, difficult to say something about the respiration of the Chaoborus larvae in the rest of the 24-hour period during their stay at the bottom and during their migration. Maybe, this species, like
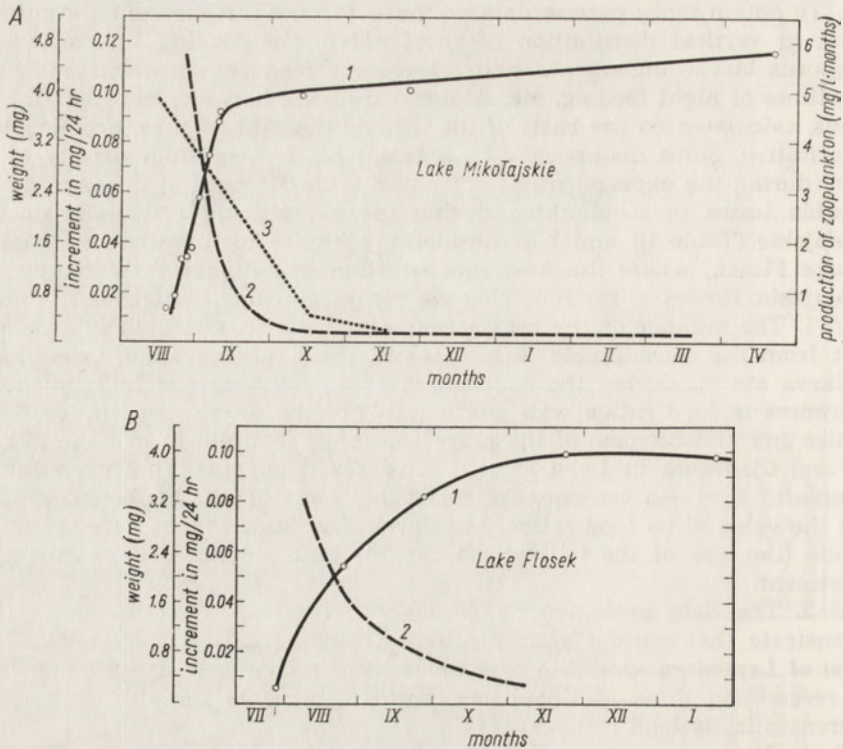
Fig. 2. Growth and increment of *Chaoborus flavicans* larvae. 1 — weight of 1 individual, in mg, 2 — increment of biomass (mg/24hr), 3 — net production of zooplankton

marine bathypelagic zooplankton species (PETIPA et al. 1967), "saves" and increases the efficiency of using the food assimilated, due to the migration towards the zone of low temperature, where the energy outlays are considerably low.

CONCLUSIONS

Late in the summer stagnation period (in mid September) the *Chaoborus flavicans* larvae reduced the daily production of crustacean zooplankton by about 50%. The daily ration of the Chaoborus individuals was from some to about a dozen or so per cent of their body weight (Table II). The use of the food consumed for growth was scarce, and amounted to less than 10%, probably due to a slow growth of Chaoborus at that time. Considerable differences in daily ration, consequently also in the efficiency of the use of food for growth were, in the two lakes investigated, a result of the differences in the size of the crustaceans consumed. Number of the individuals consumed was, in both cases, similar (one Chaoborus larva consumed, on the average, from 0.8 to 0.9 crustacean individual in 1 hr), apart from a considerable difference in the number of the crustaceans (Table I).

The period of the intense growth of the Chaoborus individuals fell on the time of a considerable abundance and of a high production of crustacean plankton (Fig. 2). (Data on the zooplankton production — according to HILL-BRICHT-ILKOWSKA and WĘGLEŃSKA 1970).

The numbers of the Chaoborus individuals in the lakes considered was fairly low, amounting to about 3000 ind./m². This form often occurs in large quantities, reaching up to 100,000 ind./m². It may be supposed that under these conditions the Chaoborus larvae much stronger affect the abundance and the production of zooplankton. COMITA and MUNRO (1969) point to a dependence of the domination and even of the occurrence of Rotatoria and Diaptomidae in pelagial on the Chaoborus pression.

Attention should also be paid to the different role of the main plankton predators: Chaoborus and Leptodora. The former one feeds on both non-predatory and predatory forms (Cyclopidae) of zooplankton, decreasing this pression on the plankton assemblage, whereas the latter one feeds only on non--predatory forms (HILLBRICHT-ILKOWSKA and KARABIN 1970). Cyclopidae were consumed by Chaoborus in both lakes, with the same intensity, irrespective of the difference in their percentage in the plankton assemblage.

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A. HILLBRICHT-ILKOWSKA and T. WĘGLEŃSKA

SOME RELATIONS BETWEEN PRODUCTION AND ZOOPLANKTON STRUCTURE OF TWO LAKES OF A VARYING TROPHY

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ABSTRACT

During the investigations carried out for two years from May to October, it was found that in the eutrophic lake (Mikołajskie) as compared with the mesotrophic lake (Tałtowisko): 1. the production of filtrators is greater (about 2 times) and among them that of microfiltrators (rotifers, Bosmina), 2. the ratio of production of predatory Cyclopidae to production of filtrators is smaller, 3. participation of hypolimnion in total lake production is greater, which is caused by great production of Bosmina in this layer.

INTRODUCTION

The aim of this study is a comparison of production and biomass of basic trophic zooplankton groups in the two lakes — mesotrophic and eutrophic, and a comparison of the share of these groups in the production of whole zooplankton of each of the investigated lakes [1].

Investigations were carried out during two years (1963, 1964) in the eutrophic Mikołajskie Lake (surface — 470 ha, max. depth 27.0 m) and mesotrophic lake Tałtowisko (surf. 326 ha, max. depth 39.5 m). Both lakes belong to the Mazurian Lakeland. The material was collected during 6 months (May–October), every 6–10 days.

METHODS

In each sample counted and measured were: developmental stages (nauplii, copepodits, juvenile cladoceran forms), adults and eggs of crustaceans, and also individuals and eggs of rotifers. The methods of estimating production were chosen depending on the species and character of basic parameters: for crustaceans — calculative method (WINBERG et al. 1965, WINBERG 1968), for egg — carrying rotifers — "linear" method of EDMONDSON (1960), and for remaining ones GALKOVSKA'S method (GALKOVSKA 1965, WINBERG

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[1] This paper is a supplement and wider approach to the investigations of: HILLBRICHT-ILKOWSKA et al. 1966. The results are due to the second year of investigations and the some new methods of production assessment.

1968)[2]. The weight of crustaceans was calculated from the size of individuals using the formulae of the relation: length-weight (HILLBRICHT-ILKOWSKA and PATALAS 1967). The weights of rotifers were determined after KOSOVA (1961) or MORDUHAJ-BCLTOVSKOJ (1954). Other parameters such as the duration of development of egg and stages and "generation time" (for rotifers) were taken after various sources[2] or own investigations (POURRIOT and HILLBRICHT--ILKOWSKA 1969).

The biomass and production were evaluated for: 9 dominant species or genera of rotifers (*Brachionus calyciflorus, Keratella cochlearis, K. quadrata, Kellicottia longispina, Filinia longiseta, Pompholyx complanata, Polyarthra* sp. div., *Synchaeta* sp. div., *Asplanchna priodonta*), 6 Cladocera species (*Daphnia cucullata, D. longispina, Diaphanosoma brachyurum, Bosmina longirostris, B. coregonii, Chydorus sphaericus*), one Diaptomidea species (*Eudiaptomus graciloides*), two Cyclopidae species (*Mesocyclops leuckartii* and *M. oithonoides*).

The above mentioned rotifers, cladocerans and *E. graciloides* belong to the basic community of non-predatory zooplankton (i.e. filtrators) for the pelagial of both lakes. The food selectivity of these animals covers particles of a various size (GLIWICZ 1968) from the smallest ones (rotifers, minor cladoceran species) to those gradually bigger ones (major cladoceran species, Diaptomidae). The both Mesocyclops species are a part of the community of pelagial predators[3]. The estimation of production and biomass of filtrators of lake

Table I. Production (*P*) and average biomass (*B*) in g/m² of non-predatory zooplankton (filtrator) and predatory Cyclopidae in Lake Tałtowisko and Mikołajskie Lake during 2 years of invesgitationss for periods of 6 months (V—X)

		Rotatoria		Cladocera		Diaptomidae		Non-predatory zooplankton (filtrators)		Predatory Cyclopidae	
		P	*B*	*P*	*B*	*P*	*B*	*P*	*B*	*P*	*B*
Mikołajskie (eutrophic)	1963	150.7	5.0	228.3	15.3	25.0	3.0	404.0	23.3	43.2	4.0
	1964	92.5	3.2	275.5	51.3	70.7	7.9	438.6	63.4	48.0	6.1
Tałtowisko (mesotrophic)	1963	62.7	1.8	131.0	7.3	16.1	1.5	213.1*	10.7	27.7	2.8
	1964	44.3	1.4	132.2	11.4	28.2	3.7	206.0*	16.6	39.2	4.6

* The production (1963 — 3.3 g/m², 1964 — 1.3 g/m²) and biomass (1963, 1964 — ~ 0.14 g/m²) of *Dreissena polymorpha* Pall. are included.

[2] A detail description of applied methods, the formulae of the dependence length-weight and data on the duration of development of various species are in the paper by HILLBRICHT-ILKOWSKA and PATALAS (1967).

[3] The rotifer species *Asplanchna priodonta* is numbered among the non-predatory zooplankton, because it was not found to feed on animal food, which is also confirmed by some literature data (GALKOVSKA 1963, POURRIOT 1965). The production and biomass of *Leptodora kindtii* — predatory species, found in both lakes — was not evaluated because of scarce material.

Tałtowisko include data on *Dreissena polymorpha* Pall. larvae (HILLBRICHT--ILKOWSKA and STAŃCZYKOWSKA 1969), which occur abundantly in this lake, however their contribution to the production of this lake is minimal (1–2%), (Table I).

RESULTS

The comparison of production and biomass values of the above distinguished trophic groups in both lakes shows that:

1) production and biomass of non-predatory zooplankton is about two times lower in mesotrophic lake than in the eutrophic one, and this difference is true for both years of investigations (Table I, Fig. 1). The differences in production and biomass of predatory Cyclopidae are much smaller, as their production and biomass in the mesotrophic lake is only 1/3–1/5 lower than in the eutrophic lake (Table I, Fig. 1).
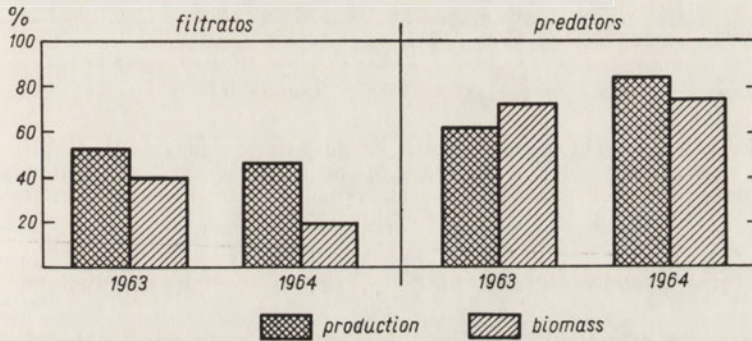
Fig. 1. Production and biomass of filtrators and predatory Cyclopidae in the mesotrophic Lake Tałtowisko in % of the respective values found for the eutrophic Mikołajškie Lake, in two successive years of investigations

2) Within the non-predatory zooplankton the greatest differences between both lakes are found in the smallest components of this group, i.e. rotifers (Table I, Fig. 2) and the two Bosmina species (Fig. 2). Production and biomass of each one of them, in the mesotrophic lake is about 1/3 (rotifers) or 1/10–1/20 (Bosmina) of respective values in the eutrophic lake (Fig. 2). However, the relatively smallest differences were between the bigger components of non-predatory zooplankton, i.e. remaining cladocerans (chiefly *D. cucullata*, *D. longispina*, *Diaph. brachyurum*) and *E. graciloides*.

The investigated lakes differ more in production and biomass of filtrators than of predators, and within the filtrators — more as to production and biomass of their smallest components, when compared with bigger ones. The character of these differences is in general similar in the two successive years of investigations despite the changes in the absolute values of production and biomass in each one lake (Table I). Similar differences in the production of filtrators and predators were obtained by PETROVICH (1968), for two Belorussian lakes: Mjastro (mesotrophic) and Batorin (eutrophic).

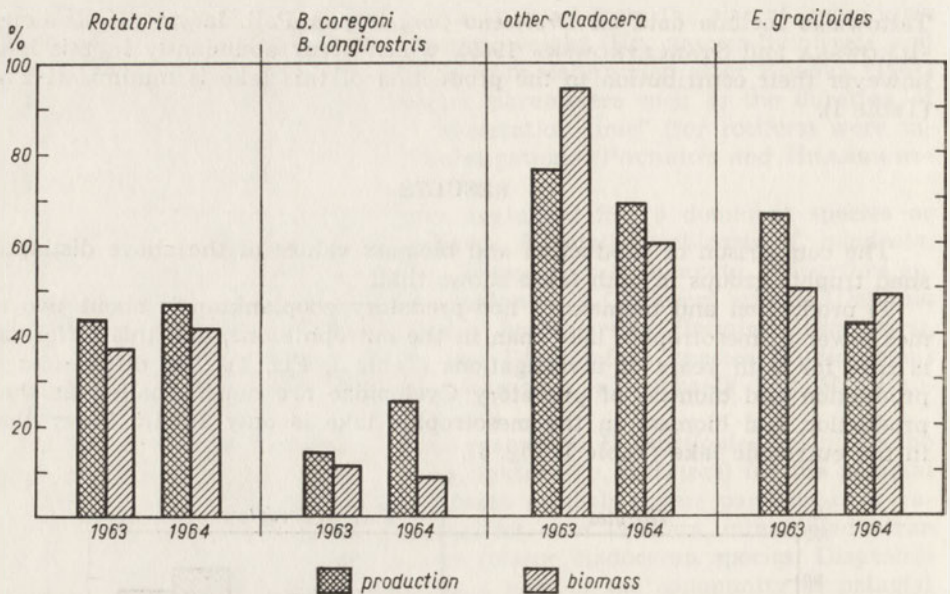Comparing the contribution of respective trophic groups of zooplankton

Fig. 2. Production and biomass of rotifers, *Bosmina coregonii+B. longirostris*, the remaining cladocerans and *E. graciloides* in the mesotrophic Lake Tałtowisko in % of the respective values found for the eutrophic Mikołajskie Lake, in two successive years of investigations

to their total production and biomass, the following conclusions may be formed:

1) The ratio of production and biomass of predatory Cyclopidae to the production and biomass of non-predatory zooplankton is 2–3 times greater in a mesotrophic than eutrophic lake (Fig. 3). This means, that independently from the differences of absolute values of production and biomass in each of these lakes, in the mesotrophic lake both Mesocyclops species are of greater significance in secondary production than in the eutrophic lake.

If we assumed the ratio of the production of these predators to the production of all filtrators as a kind of efficiency of the utilization of the production of lower trophic level by the higher one, then it is about 0.10 in eutrophic lake, and 0.13–0.20 (depending on the year of investigations) in mesotrophic lake (Fig. 3).

2) The contribution of Bosmina to the production and biomass of all filtrators is about 2–3 times higher in eutrophic lake than in mesotrophic (Fig. 4), whereas in the first year of investigations similar differences in between the lakes were noticed in the participation of rotifers in production and biomass of all filtrators (Fig. 4).

It should be, however, pointed out that in the second year of investigations, in both lakes, production and biomass of rotifers was two times lower than in the previous year (Table I). But the contribution of remaining cladocerans and *E. graciloides* in the production and biomass of the whole non-predatory zooplankton, in both lakes and years of investigations, is relatively similar. Apart from that it should be mentioned that *D. longispina* and
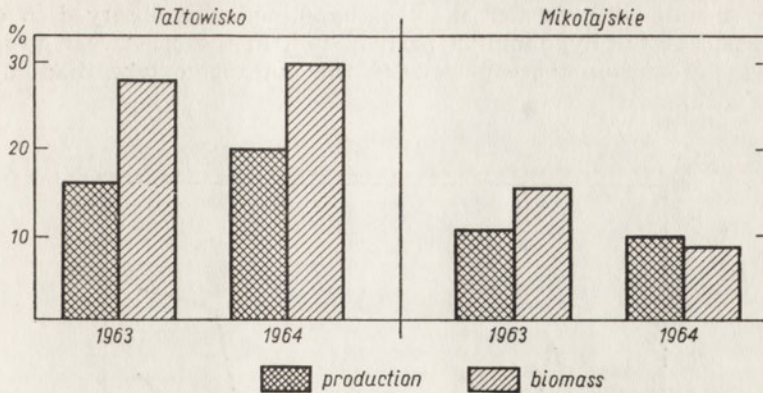
Fig. 3. Production and biomass of predatory Cyclopidae as % of the respective values for filtrators of the mesotrophic Lake Tałtowisko and eutrophic Mikołajskie Lake, in 2 successive years of investigations
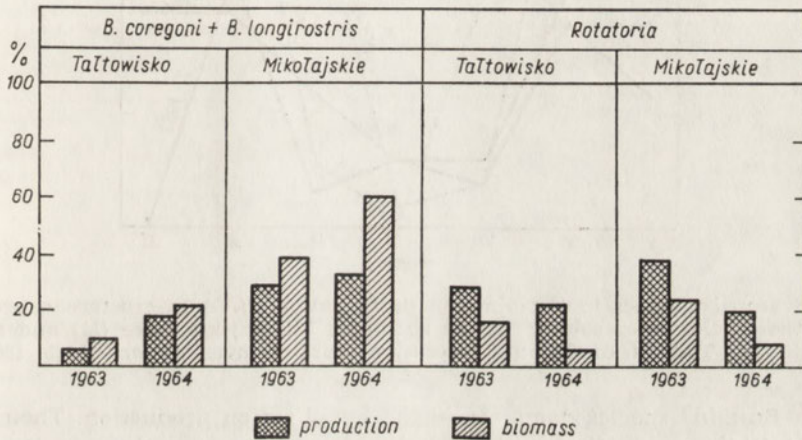

Fig. 4. The share (%) of *Bosmina coregonii* + *B. longirostris* and rotifers in production and biomass of filtrators in the mesotrophic Lake Tałtowisko and eutrophic Mikołajskie Lake, in 2 successive years of investigations

B. calyciflorus have some contribution (several per cent) to the production and biomass of the filtrators of eutrophic lake. These two species occur only in that lake.

Production assessments made separately for the three basic termic levels: epi-, meta- and hypolimnion, and then calculated per m², allow to estimate the participation of respective layers in the production of the whole water column (in the central part of the lake), and especially the participation of deeper layers, e.g. hypolimnion (below 12 m). The contribution of hypolimnetic crustacean populations to the total lake production is different for both lakes and is definitely higher (30 and 50% depending on the year of investigations) in the eutrophic lake in comparison with the mesotrophic one (respectively 15 and 20%). Also the seasonal changes of this share are different.

However in both lakes greater share of hypolimnion is observed in circulation periods, but the hypolimnion participation in the crustacean production is decidedly greater in these periods in the euthrophic lake than in mesotrophic (Fig. 5).
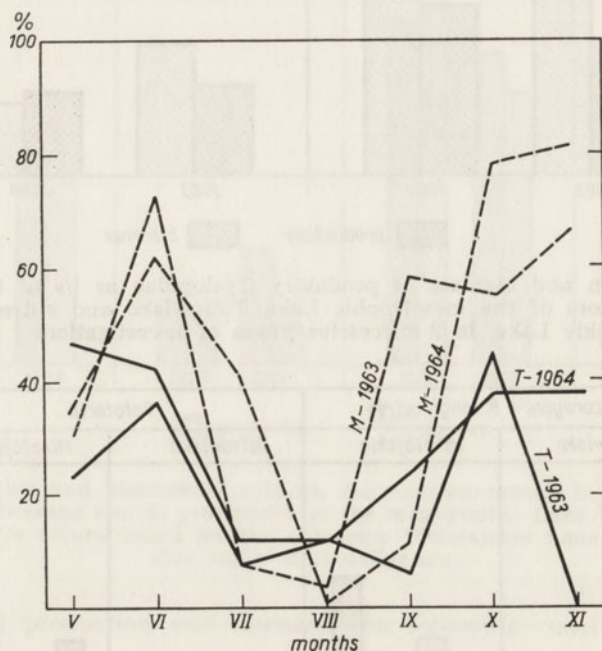
Fig. 5. Seasonal changes in hypolimnion participation ($^0/_0^0/_0$) in crustacean production of the whole water column in the eutrophic Mikołajskie Lake (M) and mesotrophic lake Tałtowisko (T), in 2 successive years of investigations (1963, 1964)

Both Bosmina species dominate in the hypolimnion production. Their contribution to the production in the hypolimnion of eutrophic lake is decidedly greater (43% and 74% in the successive years of investigations) as compared with the mesotrophic lake (20% and 45% respectively). Therefore, despite the differences in hypolimnion thickness (which is lesser in the eutropic lake), its participation in the total production of pelagial zooplankton is much greater in the eutrophic lake than in the mesotrophic lake, and the production of Bosmina decides about it.

CONCLUSIONS

The differences between the two lakes can be reduced to:

1) greater production of filtrators in the eutrophic lake, and within that of small filtrators and their greater participation in the total production as compared with the mesotrophic lake (Table I, Fig. 1, 2, 4),

2) smaller efficiency in utilizing the production of filtrators by predatory Cyclopidae in the eutrophic lake, which is probably due to similar production

of predators in both lakes but different production of filtrators (Table I, Fig. 3),

3) greater engagement of the deeper layers in the secondary production of zooplankton in the eutrophic lake, which food resources are mainly used by small filtrators — Bosmina (Fig. 5),

4) the character of these differences was maintained during both years of investigations, which seems to prove the trophic differences between the both investigated lakes.

These differences between lakes have been confirmed by results of other investigations carried out in those lakes. GLIWICZ (1968), while investigating the composition of natural food consumed by the whole zooplankton community found that the share of bacteria and fine detritus particles (several μ) was greater in the food of zooplankton from eutrophic lakes, while the share of nannoplankton was relatively small. This is the result of the great share of microfiltrators in the production of this lake. But in the zooplankton food of mesotrophic lake bigger detritus forms and nannoplankton participate more abundantly. Furthermore such composition of food consumed by zooplankton of both lakes reflects the relations within phyto- and nannoplankton. SPODNIEWSKA (1967) comparing the composition and biomass of phytoplankton of both lakes points to the domination of blue-green algae and dinoflagellates in the phytoplankton of eutrophic lake. These algae groups, because of their size, are not directly used by zooplankton. On the other hand GLIWICZ (1967) investigating the nannoplankton share in the production of the whole phytoplankton found that it is smaller in eutrophic lake than in mesotrophic lake, which in turn causes its smaller contribution to the zooplankton food.

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PRODUCTION OF EXPERIMENTAL POPULATIONS
BRACHIONUS CALYCIFLORUS PALLAS (ROTATORIA) EXPOSED TO THE ARTIFICIAL PREDATION OF DIFFERENT RATES

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ABSTRACT

Every 2–3 days 6, 25, 50, 75⁰/o of actual population size was removed (artificial predation) out of the cultures of *Brachionus calyciflorus* fed with Chlamydomonas. Together with the increase of predation rate: the average number of individuals, average life span, and the natural mortality decrease and the population fecundity, total yield and the efficiences — the ratios of the yield to the production and to the average number of individuals — increase.

INTRODUCTION

Slobodkin and Richman (1956), Slobodkin (1962, 1964) and Marshall (1967) while studying the laboratory populations of Daphnia and Hydra found a determining effect of predation on the abundance and changes in number, reproduction and age structure of the population. An analogical experiment on population of phytophagous rotifer *Brachionus calyciflorus* is presented. The populations were compared on the basis of their production estimated by three different methods. The investigations aimed at a study of the effect of predation on production of monospecies population cultured in favourable food conditions.

METHODS

11 populations of phytophagous rotifer *Brachionus calyciflorus* were the object of investigations. They were cultured in flasks, of a capacity about 27 ml, on monospecies culture of *Chlamydomonas reinhardtii*, at a temperature 18-22°C. The food was renewed every 2-3 days in such a way as to maintain the concentration in all cultures not lower than 10^4 cells/ml during the whole period of investigations (i.e. 28 days). In reality this concentration was changing in the range: 10^5-10^4 cells/ml. The initial *B. calyciflorus* population (about 12 ind./ml) originated from stabilized cultures of thermophilous strain of this species. After some 10 days of unrestrained population growth artificial predation was applied every 2 or 3 days, i.e. constant part of popu-

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lation was caught. Four variants were applied: about 25% (II variant) of the population was caught at the moment, 50% (III variant) and 75% (IV variant). In each variant there were three cultures of *B. calyciflorus*. From two cultures, used as control ones, samples were taken every 2–3 days in order to estimate the population size. Thus these populations were exposed to relatively weak predation, which was about 6% of the population size at the moment (I variant). The catches were not selective (before the catches the cultures were thoroughly mixed). After a catch the cultures were supplied with algal culture to maintain the constant volume and concentration. Every 2–3 days, in each culture the number of individuals and their eggs (number/ml) was estimated before and after the catch, and also the concentration of algae.

RESULTS

Variation in numbers and population fecundity

Changes in number of individuals and eggs (Fig. 1A, B, Table I) display a similar course in all variants of the experiment in the initial 10-day period of unrestrained population growth: at first slow and then quickened increase of the number of individuals. As soon as the catches began, differences were

Table I. Characteristics of experimental populations of *Brachionus calyciflorus* Pallas exposed to artificial predation of different rates

Parameters	Predation rate*			
	I	II	III	IV
Study period or population existence period (days)	28	28	23	20
Average number (ind./ml): before catches	243	238	51	48
after catches (residuals)	188	152	29	17
Average number of eggs/ml	66	56	14	14
Average egg/female ratio	0.27	0.24	0.30	0.36
Total yield** (ind./ml)	166	515	198	258
Total production** (ind./ml) acc. to method: "linear"	1798	1242	281	131
"exponential"	2405	1621	392	185
of GALKOVSKA	2221	1724	362	205
Natural mortality** (ind./ml) acc. to method: "linear"	1272	526	118	26
"exponential"	1870	863	212	55
of GALKOVSKA	1675	953	179	61
Population size at the end of experiment	390	295	0	0
Balance of individuals: production minus (natural mortality+yield) acc. to method: "linear"	360	202	−(35)	−(153)
"exponential"	369	243	−(18)	−(128)
of GALKOWSKA	380	256	−(15)	−(114)

* Yielding every 2 or 3 days: I — 6%, II — 25%, III — 50%, IV — 75% of actual population size was taken away.
** For the period of culture existence. Explanations of the methods applied are in the paper.

observed in respective variants*. In I and II variants a constant increase of the number of individuals was observed with only slight fluctuations, but in more intensely predated cultures — a constant decrease in numbers till the failure of culture (in the III variant after 23 days, and in the IV variant aftei 20 days since the starting of the culture). Average number of individuals (before the successive catches) is in these two variants of the experiment about 4 times lower, and the average number of residuals (after the catches) even 5–10 times lower as compared with the I and II variant (Table I).

The average egg/female ratio (Fig. 1C) (in the investigated cultures were found only females) is an indicator of population fecundity. In the initial period of unrestrained growth of all populations this indicator increases. During the predation period in the I variant (control one) it oscillates round of more or less constant level, while in cultures more intensely predated — together with the increase of predation rate — their values increase and become more variable. Therefore the average fecundity of intensely predated population (III and IV variants) is slightly higher than the average fecundity of control populations and those less intensely predated (I, II variant) (Table I).

Production, yield and natural elimination

Knowing from the previous investigations the rate of egg development of the investigated strain of *B. calyciflorus* (POURRIOT and HILLBRICHT-ILKOW-SKA 1969) and the number of eggs in each moment of population growth, the production of this population was estimated. This is taken as a difference between its size after the catch and the theoretical size after 2 or 3 days, i.e. the period between two successive catches. Thus estimated production (P_N) is expressed by the number of newly born individuals in the given period per unit of volume of the culture. Edmondson's method was used (HILLBRICHT--ILKOWSKA and PATALAS 1967) assuming:

$1°$ "Linear" growth of population:

$$P_N = N_0 \cdot B \cdot T$$

where: N_0 — population size after the catch in the t_0 moment, B — the average birth rate in the period between catches as a quotient of average number of eggs per female and the time of egg development in days, T — the period between the catches, in this case 2 or 3 days.

$2°$ "Exponential" growth of population:

$$P_N = N_0 e^{bT} - N_0$$

where: e — base of natural logarithm,

$b = \ln(1+B)$,

(other symbols as above).

For all the calculations the time of egg development was taken at 20°C. For this strain it was 14hr or 0.58 days.

For purposes of comparison the production was also estimated by method of GALKOVSKA (HILLBRICHT-ILKOWSKA and PATALAS 1967, WINBERG 1968) on the basis of "generation" time, i.e. the period of time from the egg hat-

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* Average values for the three cultures of each variant are used, as the differentiating of results was small.
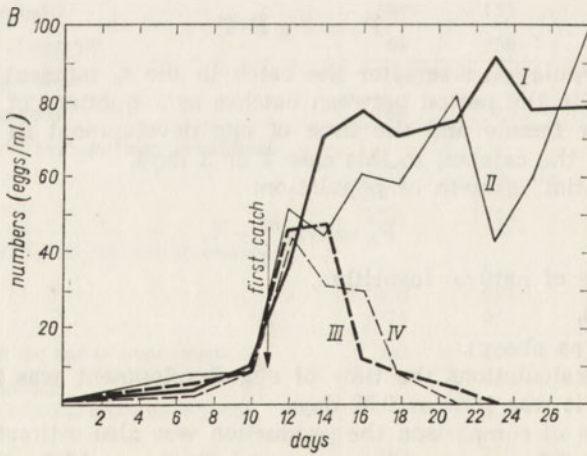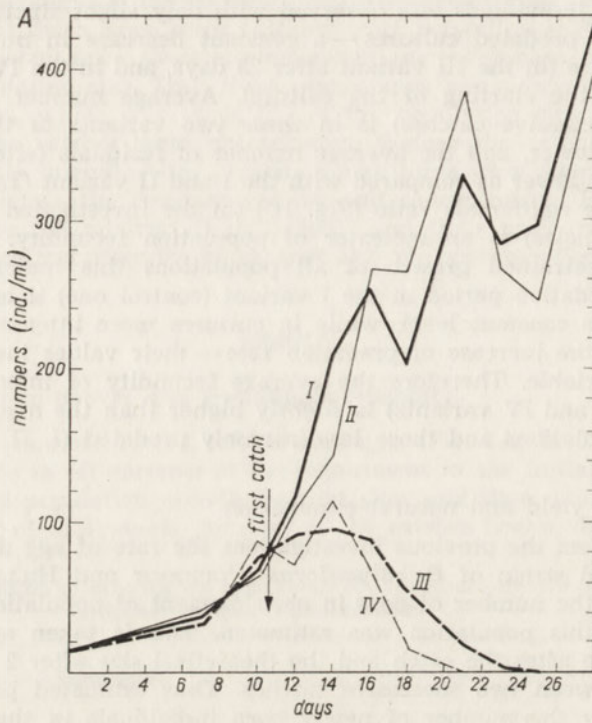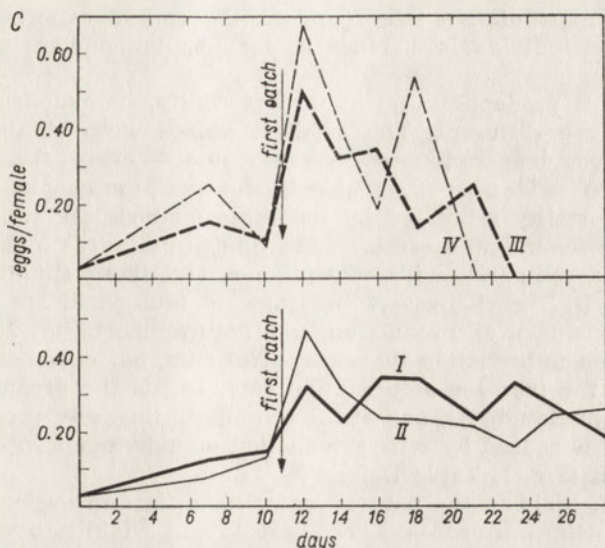
Fig. 1A, B, C. Changes in the number of individuals (A), number of eggs (B) and the average egg/female ratio (C) in experimental populations of *Brachionus calyciflorus* exposed to artificial predation of different rates. I, II, III, IV — variants of predation rates, i.e. 6% (control), 25%, 50%, and 75% of actual population size was caught every 2–3 days

ching to the hatching of the offspring's egg. For the investigated *B. calyciflorus* strain, at temperature 20°C, it is 42hr (1.8 day), (POURRIOT and HILL-BRICHT-ILKOWSKA 1969). According to this method, production (P_N) for the period T is:

$$P_N = N_0 \cdot \frac{1}{t_{e+p}} \cdot T$$

where:

t_{e+p} — the period "from egg to egg",
(other symbols as above).

Natural mortality (or elimination, as contrast of the yield) of individuals (E_N) was estimated, similarly to EDMONDSON (1960), as a difference between the theoretical population increase after the catch and the population size found before successive catches, and was expressed in the number of ind./ml:

$$E_N = (N_0 + P_N) - N_t$$

where:

N_t — population size in the moment before the successive catch,
(other symbols as above).

In very few instances (in the IV variant), in which the theoretical population increase in the period between catches was smaller than the number recorded at the end of this period ("negative" elimination) it was assumed that the natural mortality is equal to zero.

The values of production, mortality and yield for each period between the successive catches were summed, thus obtaining total production, mortality and yield per 1 ml. Together with the values of average number of indi-

viduals and the population size found at the end of experiment the basic elements of the individuals' balance in the population were obtained (Table I).

The values of production and natural mortality, estimated by three different methods are different. The smallest values were obtained using the "linear" method, bigger but relatively similar — using the "exponential" method and that of GALKOVSKA (Table I). However, the changes of production and natural mortality estimated by the three methods are similar: their values drop from several to more than ten times in cultures intensely predated (III and IV) as compared with control ones and those slightly predated (I and II) (Table I). The changes of the value of total yield are in contrast to the trend of changes of production and natural mortality. It is bigger in cultures exposed to predation than in control ones, but does not increase proportionally to the increase of predation rate, and is the greatest in cultures less intensely predated (II), and smaller in those intensely predated (III, IV) (Table I). This is caused by strong reduction of individuals in cultures intensively predated (Fig. 1, Table I).

The ratio of yield to the natural mortality differs in variants (Table I) — it is smallest (10%) in control ones, greater in slightly predated cultures (II — about 54-90%, depending on the method estimating the natural mortality), but in the III variant it is practically equal to natural mortality, whereas in most intensely predated cultures (IV) the yield is several times higher than the natural mortality (Table I).

The sum of natural mortality (Table I) is the total mortality of individuals. Subtracting this value from production (Table I) gives in the I and II variant a number approximate to the population size recorded at the end of experiment (Table I), however in the III and IV variant the natural mortality together with the yield are greater than the productive abilities of population which in effect leads to the failure of the cultures (Table I, II).

The ratios between production, yield, natural mortality and average number of individuals

The ratio of production to the average number of residuals after catches (so-called P/B coefficient, commonly used) is an indicator of production rate in a given period. The values of this indicator are almost constant in all variants (about 10) (Table II), i.e. the production was about 10 times higher than the average numbers of individuals left after the catches. However, the both yield efficiences, i.e. the ratio of yield to the average number of residuals and the ratio of yield to production (Table II), increase together with the increasing predation rate. The least productive in that sense are the control populations, slightly predated. In the II variant (25% catch) the total yield exceeds three times the average number of residuals and is about 1/3 of the total production of these populations. In the III variant (50% catch) it is seven times higher and is at least half of the production, and in the IV variant (75% catch) it is 15 times bigger than the production of these populations (Table II).

In our experiments the removals were one of the two factors of mortality (= elimination) of individuals. Changes in the ratio of natural mortality to production behave in contrast to changes in the ratio of yield to production (Table II). In the control variant about 75% of production compen-

Table II. The ratios between production, yield, mortality and average number of individuals in populations of *Brachionus calyciflorus* exposed to artificial predation of different rates

Ratio	Predation rate*			
	I	II	III	IV
Production/average number of residuals, acc. to method:				
"linear"	9.6	8.2	9.7	7.7
"exponential"	12.8	10.7	13.5	10.9
of GALKOVSKA	11.8	11.3	12.5	12.1
Yield/average number of residuals	0.9	3.4	6.8	15.2
Yield/production (in %) acc. to method**:				
"linear"	9	41	70	(197)
"exponential"	7	32	50	(140)
of GALKOVSKA	7	30	55	(126)
Natural mortality (production in %) acc. to method:				
"linear"	71	42	42	20
"exponential"	78	53	54	30
of GALKOVSKA	75	55	49	30
Total morality/production (in %) acc. to method**:				
"linear"	80	83	(112)	(217)
"exponential"	85	85	(104)	(170)
of GALKOVSKA	82	85	(104)	(156)

* See the explanations, Table I.
** Acc. to the method of production estimation; explanations of the methods applied are in the paper, values above 100% are in brackets.

sates the natural mortality as the yield of these populations is minimal. In the II and III variant half of the production compensates the mortality, while in the IV variant where the chances of surviving the catches are the smallest the significance of natural mortality is small (Table II). In the most intensely predated cultures (III and IV) the production during the research period does not cover all the losses of individuals, i.e. catches and natural mortality (Table II), which in result causes a constant decrease in numbers of individuals till the failure of cultures.

Average life duration of individuals

From the total mortality and average number of residuals the average period of their turnover, T_N was estimated, which is the average life span (HILLBRICHT-ILKOWSKA and PATALAS 1967, PETRUSEWICZ 1966, 1966a)

$$T_N = \frac{\bar{N} \cdot T}{E}$$

where:

$\bar{N}$ — average number of residuals per 1 ml,

E — total mortality (elimination) per ml in the period T,

$\bar{T}$ — study period.

The turnover period $\bar{T}_N$ differs according to the applied method of estimating the natural mortality (Table III), but is in general 3–4 days for the I and II variant, whereas 1–2 days for the III and IV variant. The last value is smaller than the "generation time", which at the temperature 20°C is about

Table III. Period of turnover of individuals i.e. their average life span (in days), in *Brachionus calyciflorus* populations exposed to artificial predation of different rates

Method of estimating mortality**	Predation rate*			
	I	II	III	IV
EDMONDSON'S "linear"	3.7	4.0	2.1	1.2
"exponential"	2.6	3.1	1.6	1.1
GALKOVSKA'S	2.9	2.9	1.8	1.1

* See the explanations, Table I.
** See the explanations of methods in the paper.

1.8 day. And so the average chances of surviving of individuals in intensely predated populations were usually smaller than the reproductive abilities of these populations.

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PRODUCTION AND CONSUMPTION IN THE POPULATION OF *ASPIUS ASPIUS* (L.) OF THE VISTULA RIVER

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ABSTRACT

Production, consumption and related vital statistics for the predatory fish population of *Aspius aspius* sampled from the middle course of the Vistula River were calculated and discussed. Turnover rate, i.e. the ratio P/B was low (0.5). This might be related to the longevity of the fish individuals. The population produced about 0.135 kcal/m²·year, while it consumed about 10 times as much. Although the consumption per unit area was small, it could be considered significant for the energy flow in the ecosystem, since *Aspius aspius* was one of the most abundant terminal consumers.

INTRODUCTION

Scarce data on production and consumption of fish populations under natural conditions prompted the present author to use the available materials for estimation of these processes in the predatory fish population in the Vistula River. This paper is an attempt at presenting both methods and results of the estimation made for the population of one of them, viz. *Aspius aspius* (L.).

In the period between 1952 and 1958 the average annual catch of *Aspius aspius* in the middle course of the Vistula River was 13.6 tons, i.e. about 4⁰/₀ of the total commercial catch.

HOROSZEWICZ (1964) found that *Aspius aspius* individuals larger than 20 cm in length fed on small fish exclusively. Hence, the population of *Aspius aspius* was subdivided into two parts: younger (smaller) fish individuals, which were in the pre-predatory or transition phase, and older fish individuals — in the predatory phase. Incidentally, such a subdivision is almost identical with the subdivision into a pre-exploitation part (phase) of the population, and into that exploited by men. The material collected allowed the production and consumption to be estimated only as concerns the second part, i.e. the fish individuals in the predatory phase.

MATERIAL

The present study was based on the materials collected in the period from 1955 to 1957 in a 560 km long section of the Vistula River, from the San River mouth to the Montawa River mouth. These materials were already utilized by BACKIEL (1962, 1964), HOROSZEWICZ (1964). Moreover, samples collected in 1964 and 1965 from the Vistula River at Włocławek were analysed, as well.

RESULTS

ESTIMATION OF BASIC PARAMETERS

Age determination of the fish individuals in their predatory phase of life, analysis of their average increase in weight, and calculation of the fish abundance in the successive age groups were necessary to estimate the production of *Aspius aspius* in this phase.

It has been accepted on the results of study on the age, growth (BACKIEL 1964) and food of fish (HOROSZEWICZ 1964) that the phase of predatory life of the *Aspius aspius* individuals lasts from age 2 to age 13.

The growth in weight could be presented by means of the von BERTA-LANFFY's equation as follows:

$$w_t = 17,740[1 - \exp 0.080425(t - 0.130)]^3$$

where:

w_t — average weight of an individual "t"-years-old,

exp means "e" (base of natural logarithms) to the power shown after exp,

t — age of fish in years.

This equation does not describe the course of growth within a year. It was assumed that the fish individuals grew ony in a period from April to October inclusive (BACKIEL 1962), and that in this period the increase in weight was the exponential time function. In a period from November to March the fish individuals did not grow at all.

Abundance. Age composition (or "catch curve") of samples of the exploited population collected in the period 1955–1957 served for the estimation of total mortality of fish in ages from 6th to 13th years. The annual mortality was found to be 47%, and the total mortality coefficient $Z = 0.635$ (BACKIEL 1964). The material of 180 specimens collected in 1964 and 1965 enabled to estimate the mortality coefficient again. Assuming that the growth rate of *Aspius aspius* had not changed since 1957 an equation suggested by BEVERTON and HOLT (1956) was applied to this collection and to the material of 1955–1957. The equation relates Z (total mortality coefficient) to certain known quantities as follows:

$$Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l'}$$

where:

K — coefficient from BERTALANFFY's equation of growth ($= 0.080425$),

L_∞ — ultimate length from this equation ($= 110$ cm),

$\bar{l}$ — average length of fish in a sample, in which the smallest length of fish equally vulnerable to net equals l'.

The results of the computations by means of this method are as follows:

Sample	Coefficient of mortality Z	Survival S
1955/1957	0.6493	0.5224
1964/1965	0.6553	0.5196
Estimation from catch curve	0.635	0.53

Differences among the estimates of Z are small and statistically insignificant[*]. It can be inferred from the estimates of Z that the preliminary estimate Z = 0.635 (c.f. BACKIEL 1964) is subject to a rather small error and that between the years of collecting materials (from 1955 to 1965) the mortality of the older fish remained essentially constant.

The above estimate concerns older than 6 years-old-fish. Total mortality of younger fish could be estimated after assessing the fishing mortality.

PLISZKA (1951) tagged and released 34 specimens of *Aspius aspius* into the Vistula River cut which 8 fish were recaptured during one year at large. According to the exponential model:

$$Z = F + M$$

and

$$F = \frac{1 - \exp(-F - M)}{F + M} = \frac{8}{34}$$

where F and M are fishing and natural mortality coefficients respectively, Z — as before.

Hence, if Z = 0.635 then F = 0.3179 or approximately 0.32, therefore M = 0.315.

Due to small numbers of tagged and recaptured fish the reliability of the estimate of F is low. However, the F coefficient computed for chub using PLISZKA'S (1951) data equaled 0.35, and this coefficient based on mass tagging of *Vimba vimba* in the Vistula River ranged from 0.39 to 0.53 (BACKIEL unpublished data).

Estimations of F and Z for all age groups of *Aspius aspius* in the predatory phase (from age 2 to age 13) could be obtained from the age composition in samples assuming that F in age groups from 6 to 13 equaled 0.32 and that the natural mortality (M) in younger fish (from age 2 to age 6) was the same as that in the older ones.

Using informations on individual growth in weight, on natural and fishing mortalities and on the effect of the latter mortality being the average annual catch of *Aspius aspius* viz. 13.6 tons abundance and biomass of the fish population could have been estimated.

COMPUTATION OF PRODUCTION

In the exponential model of growth and mortality, the annual production (P), realized in the course of 7 warm months, of an age group t per 1 individual of age 2 ("recruit") equals to:

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[*] Standart error (S.E.) of the coefficient of mortality "Z" in *Aspius aspius* was not calculated. This error, however, was assessed for the estimations of survival (S) in the populations of *Leuciscus cephalus* L.:

$$S = 0.4854; \quad S.E. = \pm 0.03025$$

and of *S. lucioperca*:

$$S_1 = 0.4239; \quad S.E. = \pm 0.02228$$

$$S_2 = 0.4554; \quad S.E. = \pm 0.01782.$$

There is no reason to suppose that the standard error of estimation of survival in *Aspius aspius* is smaller than the above shown standard errors.

$$\frac{1}{R}P_t = \frac{1}{R}G_t \cdot \frac{w_t N_t \left[\exp\left(G - \frac{7}{12}Z\right) - 1\right]}{G_t - \frac{7}{12}Z},$$

where:

$G_t = \log_e w_{t+1} - \log_e w_t,$
R = number of recruits,
N_t = abundance of the age group t.
Other symbols as given previously.

According to this model the annual catch (in weight) of the individuals of the age group t per 1 "recruit" amounts to:

$$\frac{Y_t}{R} = F_t \cdot \bar{B}_t$$

($\bar{B}_t$ = average biomass of the age group t).

The sums of $\frac{1}{R}P_t$; $\frac{1}{R}Y_t$; $\frac{1}{R}\bar{B}_t$ for t from 2 to 12 are, of course, respectively: production, catch, and average biomass per 1 individual at age 2 ("recruit") for the predatory fish population and amount, in grams, to 541.6, 242.1, and 1100.6, respectively.
Hence:

$$\frac{P.}{\bar{B}.} = 0.493; \qquad \frac{Y.}{\bar{B}.} = 220$$

(dots denote estimates for the entire population).

It was also possible to calculate the biomass of the individuals recruited (B_R), into the predatory population (i.e. those being two-year-old), in relation to the average biomass. This ratio is as much as 0.045. Finally, the biomass of fish which died annually (B_M) was found. If the population is in a steady state in which the losses of biomass are compensated by the "income" (recruitment) of young fish and by the growth (production) then:

$$P. + B_R = Y. + B_M.$$

Taking $\bar{B} = 1$ we obtain:

$$0.493 + 0.045 = 0.220 + 0.318.$$

The average annual catch (equal to 13.6 t) from the middle course of the Vistula River (570 km in length, an area amounting to about 22,600 ha) was a basis for the calculations that resulted in the following data:

Average biomass of predatory
Aspius aspius individuals $\bar{B}$. 61.8 t — 2734.5 g/ha,
Annual production of these fish P. 30.47 t — 1348.2 g/ha,
Recruitment B_R 2.78 t — 123.0 g/ha,
Annual catch Y. 13.60 t — 601.7 g/ha,
Annual death biomass B_M 19.65 t — 869.5 g/ha.

As compared with the similar estimates made by the other authors (CHAPMAN 1967) these are very small values.

The "turn-over", i.e. the $P/\overline{B}$ ratio, amounts to 0.493. This means that the "exchange" of the whole biomass requires slightly more than two years. $P/\overline{B}$. ratios, compiled by CHAPMAN (1967) for some fish populations ranged from 1 to 2.5, but they concerned whole populations (begining with the youngest stages) and the fishes of short life spans. The production (P) to catch (Y) ratio was, according to various authors, between 2 and 15, and in the case of the predatory population of *Aspius aspius* it was 2.24.

The result of the calculation of a hypothetical production of the population of young *Aspius aspius*, seems interesting. This part includes fish from the beginning of feeding to the age of 2 years, when they weigh 50.2 g on the average.

This can be done only under certain assumptions, e.g.:

time (t), in years	0	1/4	1	2
weight (w), in grams	0.02	1	6	50.2
survival (S)		0.02	0.3	0.3
relative number (N)	555	11.1	3.3	1

Biomass and production of this hypothetical pre-predatory phase of the population computed with the aid of the exponential model can be simply added to the respective quantities for the predatory phase taken per recruit (at age 2) and now those sums result in:

$$\frac{P.}{B.} = 0.592.$$

It may be seen here that this ratio increased, but it is still considerably smaller than the ratios found to appear in other fish populations. Most probably the populations, in which the production of numerous age groups (10 and more) cumulates, have small $P/\overline{B}$. ratio, hence, a low turn-over rate.

CONSUMPTION OF THE POPULATION OF *ASPIUS ASPIUS*

The materials collected allowed to estimate the annual consumption (C) by the predatory part of the population of *Aspius aspius* by means of two methods. The first method consists in using WINBERG's equation (1956):

$$C = 1.25\,(\Delta w + \text{Resp.}),$$

where:

C — food consumed during a short period of time,
Δw — increase in body weight,
Resp. — metabolism (all variables expressed in the same units).

According to WINBERG (1956, 1961), the resting metabolism of the fresh-water fish at temperature of 20°C can be calculated from the following relationship:

$$\text{Resp.(ml O}_2\text{/hr)} = 0.3\,w^{0.8},$$

where:

w — weight in grams,
Resp. — consumption of oxygen in ml/hr.

The effect of temperature on metabolism was taken into account by using Krogh's curve. In order to express metabolism in terms of biomass or of energy of fish ingested by the predator it was assumed that 1 cal corresponds to

1 mg wet weight and to 5 ml O_2. In the WINBERG's equation applied to a fish population, the increase in body weight becomes production (P). The metabolism concerns all individuals which change their weight and number during the year. The annual changes in the average fish weight and in the abundance of the individual age groups were calculated in the same way as in the case of production computation.

According to suggestions of WINBERG (1956) and MANN (1965), the resting "Resp." was doubled to obtain the probable level cf active metabolism. The calculations were made by a computer and resulted in the quantities (per year):

Active metabolism	— 3811.8 kcal/recruit
Production	— 541.6 kcal/recruit
Non-assimilated energy	— 1088.4 kcal/recruit
Consumption (C.)	— 5441.8 kcal/recruit

$$\text{Ratios:} \quad \frac{P.}{C.} = K_1 = 0.1; \quad \frac{C.}{B.} = 4.95; \quad \frac{Y.}{C.} = 0.045.$$

Another method applied for computation of ccnsumption is based on the following relationship:

$$r = \frac{24 \cdot r_a}{h}$$

proposed by BAYKOV (1935), where:
r — daily food ration,
r_a — amount of food found in the alimentary canal,
h — fcod passage (in hours) through alimentary canal.

While examining the food of fishes, HOROSZEWICZ (1964) determined the weight of food (r_a) in $^0/_0$ of the fish weight, and the degree of digestion according to an arbitrary scale (from degree I to V). The average degree of digestion amounted to III, i.e. the food found in the alimentary canals was half-digested. Hence, it can be assumed that the food consumed must have been twice as heavy as the food actually found.

Average r_a values depend upon the size of fish and the season of the year. This relationship could be expressed by the following equation, on the basis of unpublished data of HOROSZEWICZ:

$$r_a = a - 0.0205\, l,$$

where:
r_a — weight of food in $^0/_0$ of fish body weight,
a — a constant for winter season = 1.291, spring season = 1.751, summer season = 1.671, autumn season 1.381,
l — length of fish, in cm.

By multiplying the r_a values calculated for the seasons of the year and for the average length of fish of successive age groups by the average biomasses of these age groups the amounts of food in the alimentary canals of these age groups in the seasons (per biomass unit) were obtained. The sums of these amounts for individual age groups (from 2 to 12) gave the contents of the alimentary canals of the whole predatory population in the successive seasons as per cent of biomass.

The likely values of "h", i.e. of the food passage rate were determined

(Fig. 1) on the basis of few data reported by various authors. Figure 1 demonstrates that the value "*h*" distinctly depends upon the temperature. Krogh's curve seems to express adequately this relationship.

The data presented in Fig. 1 also suggest that the digestion process in the predatory fish is slower than that in the non-predatory ones.
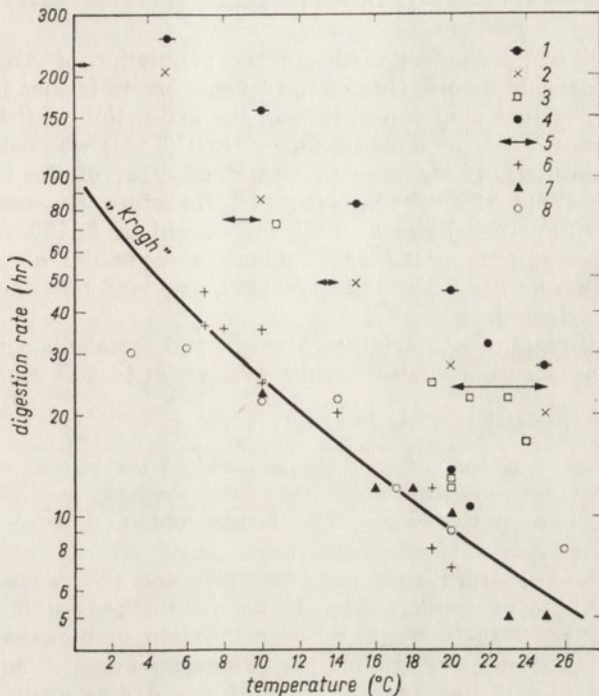

Fig. 1. Relationship between the rate of food passage through the alimentary canals of fish and temperature for several fish species: 1 — *S. lucioperca* (FABIAN et al. 1963), 2 — *Silurus glanis* (FABIAN et al. 1963), 3 — *Esox lucius* (FORTUNATOVA 1955, MANTEJFEL 1965), 4 — *S. lucioperca* (MANTEJFEL 1965), 5 — all predators (POPOVA 1967), 6 — *Misgurnus fossilis* (SCHEURING 1928), 7 — *Rutilus rutilus* (small) (KARZINKIN 1932), 8 — *Rutilus rutilus caspicus* (BOKOVA 1940)

Estimations of the food passage rates are far from being precise, and subject to large error (compare e.g. MANTEJFEL 1965, WINDELL 1967). However, accepting that the digestion rate of the *Aspius aspius* individuals resembles that of Cypriniformes, i.e. $h = 9$ hours at a temperature of 20°C, or it is slightly slower than among the predatory fish, e.g. $h = 13$ hours at a temperature of 20°C (Fig. 1), the consumption can be calculated in two variants. The average food passage rates in successive months were determined from the average temperatures cf the Vistula River water. Consumption calculated in this way amounts to:

$$\text{if } h_{20°} = 13 \text{ then } C = 4140 \text{ gram/recruit,}$$
$$\text{if } h_{20°} = 9 \text{ then } C = 5886 \text{ gram/recruit.}$$

It should be kept in mind that the estimation of consumption made by means of WINBERG's method gave a result that amounted to 5442 g, i.e. an in-

termediate quantity between those arrived at above. It may be inferred from this that the consumption of the population of *Aspius aspius* was estimated with a reasonable accuracy and that it amounts to about 13,400 kcal/ha, or 1.34 kcal/m²·year.

DISCUSSION

The estimates of parameters made for the population of *Aspius aspius* are subject to considerable errors. One of the largest errors is that inherent in the estimate of the absolute abundance, thus in the estimation of fish biomass, too. If the ratio of recaptured to released tagged fish (8 : 34) was considered a measure of the exploitation rate then the standard error of the estimate of the latter would be about 31% of that estimate. Therefore, the confidence limits for the estimated average biomass 0.2734/m² would be 0.1730 and 0.7320, and consequently broad limits would be obtained for estimates of production and consumption (from 0.63 to 2.65 of the average), provided that the other sources of errors are neglected.

Since the estimations of mortality, growth, and metabolism were also subject to errors the accuracy of the results arrived at in this study, of the primary quantities in particular, is low; the ratios $\frac{P.}{B.}$ and $\frac{P.}{C.}$ seem to be more accurate. Thus any interpretation must be made with utmost caution.

In view of the expected low accuracy of the methods applied, the consumption was computed in two ways. The results obtained were fairly similar, although the methods of assessment were based on not entirely justified assumptions. These results justify the possibility and the necessity of conducting studies on the consumption using these two methods simultaneously; but particular attention is to be paid on the estimation of biomass.

The results of the calculations may diagrammatically be presented in Fig. 2, provided that the average biomass of the *Aspius aspius* population is constant, thus the whole system is balanced. Energy that flows annualy through the predatory population of *Aspius aspius* is five times the energy content of the mean biomass, and men use only 4.5% of this energy. Ecological efficiency $\left(\frac{P.}{C.}\right)$ amounts here to 10%.

This population returns to the environment about 20% of the energy consumed, in the form of the unassimilated matter (excreta and faeces) and about 6.4% — in the form of the dead fish, both during the year.

An interesting comparison can be made as follows: consumption of the predatory population of *Aspius aspius* in the Vistula River — 1.3 kcal/m²·year, consumption of the non-predatory fish individuals in the Thames (according to MANN 1965) — 704.5 kcal/m²·year, primary production of rivers — from 0.1 to 1.0 Cg/cm²·day, or that of estuaries — 4.4 of dry matter/m²·day, i.e. about 350–6400 kcal/m²·year (ODUM 1954, OPOROWSKA 1966).

This rather risky compilation of data implies that the flow of energy through the population of *Aspius aspius* is negligible, thus its role in the ecosystem is unimportant. Even if the evaluation of consumption was considerably underestimated, the energy flow would still be relatively small. These fish, however, consumed other ones that fed on the bottom invertebrate and plank-
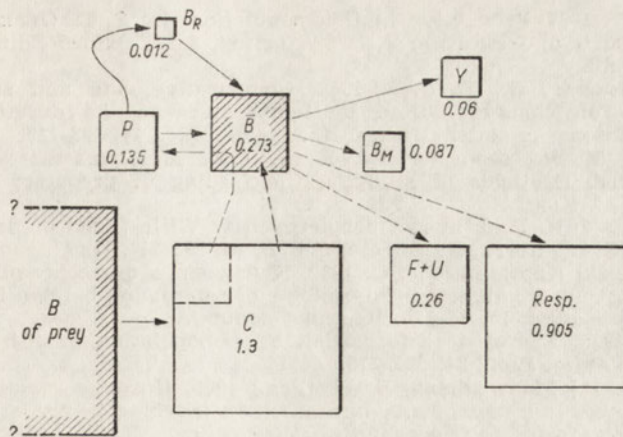
Fig. 2. Flow of energy and of matter through the population of *Aspius aspius* in its predatory phase in the Vistula River. Continuous lines indicate the flow without any change in the form of matter; broken line — the flow with a change in the form of matter. Numbers in figure: kcal/m²·year. Part of the unknown biomass *B* of prey is consumed ("C" = about 1.3 kcal/m²·year) by the biomass of *Aspius aspius* in the state of equilibrium ($\bar{B}$ = 0.273 kcal/m²).To this biomass come new young fish individuals from the pre-predatory phase (B_R = 0.012 kcal/m²· ·year) and the biomass produces then *P* = 0.135 kcal/m²·year. Catch is *Y* = 0.06 and B_M = 0.087 kcal/m²·year dies out. The unassimilated energy amounts to (*F*+*U*) = 0.26 kcal, and the losses on metabolism are Resp. = 0.905 kcal/m²·year

ton organisms. Among them were detritophagous animals, filtrators, and predatory or phytophagous animals. Any speculation on the quantitative aspect of this trophic pyramids leads to a conclusion that there are several trophic levels between the primary production and the consumption by *Aspius aspius*. Multiplying each of these levels by the respective ecological efficiences, one can realize that the consumption by the population of *Aspius aspius* (approximately 1.3 kcal/m²·year) proceeds "at the cost" of a primary production, say, 1000 times greater than the estimated consumption, and that the role of this population in the ecosystem is, after all, very important.

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C. Felińska

LIPIDS AND CHOLESTEROL IN BLOOD SERUM OF BULLTROUT FEMALES (*SALMO TRUTTA* L.) IN TWO VARIOUS STAGES OF SEXUAL CYCLE

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ABSTRACT

Total fat, fat fractions, aliphatic acids (from C_{14} to C_{22}) and total cholesterol contents have been determined in blood serum of the females of bulltrout (*Salmo trutta* L.), the gonads of which were in the III stage of maturity (according to Maier's scale) and during the artificial spawning. It has been ascertained that during the spawning-season a statistically important decrease (by 58%) in total fat amounts may be noted. At the same time both fraction of glycerides and total cholesterol increase by 29%.

INTRODUCTION

The problem of wandering of the fish individuals of the family Salmonidae for spawning is related to the morphological and physiological changes of these animals. Beside the physic-chemical changes in blood (ROBERTSON et al. 1961), also a decrease in body weight, and a growth of sex glands may be observed (SZMIDT 1950).

The purpose of this work was to present some interrelations that exist between the development of sex glands and fat amounts, fat fractions, and total cholesterol in the blood serum of the bulltrout females.

MATERIALS AND METHODS

The research compared twenty two "Baltic" bulltrout females (*Salmo trutta* L.) fished in River Rega, near Trzebiatów. In June, the length of the females (L.c.) ranged from 57 to 75 cm (66.5 cm on an average), in December, in turn, from 57 to 80 cm (i.e. 64.6 cm on an average). Blood for analysis was for the first time taken in June from eleven females, the gonads of which were, according to Maier's scale, in the III stage of maturity, and then in December, during the period of artificial spawning. Blood samples were taken from bulb of aorta, and then their total fat amounts, fat fractions, higher aliphatic acids and total cholesterol were determined.

Fat from the blood serum was extracted according to BLIGH and DYER

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Table I. Total fat, aliphatic fractions and total cholesterol in blood serum of bulltrout

| Serial number of fish | Total fat | Aliphatic fractions | | | | Total cholesterol |
		Glice-rides	Phospholipids	Sterol esters	Free aliphatic acids	
1	2126	977	615	228	306	414
2	2132	826	673	315	318	382
3	2108	905	604	281	318	430
4	2092	906	573	296	318	382
5	2339	946	826	294	273	351
6	2126	977	613	228	306	373
7	2369	929	746	282	412	352
8	2059	885	672	256	246	386
9	2101	936	740	164	261	378
10	2233	925	679	226	403	372
11	2413	1003	800	214	396	—
X̄	2191	929	685	253	323	381
	±119	±49.4	±61.4	±44.5	±55.0	±26.0

The heading "June" spans the table.

(1959). The total fat underwent separation on column with silica gel on celite in a ratio 3:1. Neutral fat and free aliphatic acids were eluated with chloroform, and phospholipids — with a 1:1 chloroform-methanol solution. The neutral fat was separated again on column by means of 1% light petroleum in light petroleum to obtain sterol esters. Glycerides were eluated with ethyl ether only. The analysis of the methyl ester of aliphatic fats (from C_{14} to C_{22}) was made by gas chromatography method (Pye Argon Chromatograph, England). Column: adipiniane of ethyl glycol (HJ-EFF-2A) 10% on celite 545. Temperature 190°C, voltage — 1250 V, argon flow — 40 ml/min, size of sample — 0.1 l. Identification of the individual acids on the chromatograms obtained was performed by comparing retention times of methyl esters of standard acids. The calculation of the percentage composition of the aliphatic acid mixture was made by triangulation method. Nomenclature of acids was taken according to Dole et al. (1959). Total cholesterol in blood serum was determined by colorimetric method (Stefaniak and Januszkiewicz 1962).

RESULTS

The amounts of total fat, its fractions, and the amounts of total cholesterol in blood serum of the bulltrout females in June and December are illustrated on Table I; composition of aliphatic acids (from C_{14} to C_{22}) in blood serum of the bulltrout females — on Table II.

DISCUSSION

The total fat in 100 ml of blood serum of the bulltrout females amounted in June to 2191 mg on the average, and during the artificial spawning — 1277 mg, this being 58.74% of the value obtained in June. This difference may

(*Salmo trutta* L.) females in two various periods of sex cycle (mg/100 ml of serum)

| Serial number of fish | Total fat | December | | | | Total cholesterol |
| | | Aliphatic fractions | | | | |
		Glice-rides	Phospho-lipids	Sterol esters	Free aliphatic acids	
12	1545	760	333	320	132	489
13	1172	518	390	164	100	498
14	1389	786	314	204	85	508
15	1477	836	370	167	104	472
16	1193	629	273	234	57	476
17	1098	587	272	132	107	504
18	1074	644	210	147	73	532
19	1118	449	440	166	69	532
20	1363	720	333	203	107	489
21	1276	604	437	195	40	504
22	1339	664	407	207	61	—
X̄	1277 ±154	654 ±114	343 ±72.6	194 ±51.2	84 ±27.0	492 ±22.5

Table II. Aliphatic acids in blood serum of bulltrout (*Salmo trutta* L.) females in % of the total amount of acids in the individual fractions

| Aliphatic fractions | Aliphatic fractions | | | | | | | |
| | Glycerides | | Phospho-lipids | | Sterol esters | | Free aliphatic acids | |
	A[1]	B[2]	A	B	A	B	A	B
C_{14}	6.00	2.33	1.73	0.80	1.50	2.17	1.78	3.72
$C_{16:0}$	10.07	13.63	50.25	43.02	31.31	26.60	30.80	16.50
$C_{16:1}$	4.64	6.09	5.72	6.63	5.54	2.50	5.40	5.77
$C_{18:0}$	1.44	1.30	14.21	10.98	13.09	13.72	14.20	3.50
$C_{18:1}$	47.48	48.77	21.49	33.86	38.28	41.87	42.84	63.90
$C_{18:2}$	2.88	3.11	traces	1.14	—	4.33	traces	2.80
C_{20}	2.54	1.94	5.20	traces	traces	traces	2.84	0.80
C_{22}	24.95	21.40	—	3.55	6.04	traces	traces	1.74
Others[3]	—	1.43	1.40	traces	4.24	8.81	2.14	1.27

[1] — June; [2] — December; [3] — acids with odd numbers of carbon and those of uncertain structure.

depend upon numerous factors such as quantity and quality of food, development degree of sex glands, hydrographic conditions, etc. (ELWERTOWSKI and MACIEJCZYK 1959). The opinions concerning the consumption by bulltrout individuals during their spawning wandering and during the spawning-season are controversial. According to the recent studies made by CHEŁKOWSKI (1968 — unpublished), alimentary canals of the bulltrout individuals from River Rega were in June filled in with food composed of marine fish remains (mainly herrings). In December, however, only scarce amounts of food were ascertained, or food was absent at all. Thus, at that time the fish uses its energy

accumulated in the triglycerides of fatty tissue. Liberation of free aliphatic fats into blood is stimulated by the following factors: adrenaline, nor-adrenaline, glucagon, cortycotropin, tyreotropin, gonadotropin and many others (Korniszewski and Krotkowski 1967). As yet, the list of the lipolytic factors is not complete. Both synthesis and decomposition of the triglycerides in fatty tissue are controlled not only by hormones here. Of considerable importance is also nervous system there.

The lower amount of total fat ascertained in the blood serum of *Salmo trutta* L. during the spawning-season suggests a question, whether the decrease has been proportional in all the fractions considered, or in some of them only.

In June, the aliphatic acids in blood serum of the bulltrout individuals appeared, in about 85%, in the esterified form. The percentages of the most important fractions were here as follows: glycerides — 42.44% on the average, phospho-lipids — 31.28%, sterol esters — 11.5%, and free aliphatic acids — 14.7%, as compared with the total amounts of the fractions examined.

During the artificial spawning 95.5% of the aliphatic acids appeared also in the esterified form. Glycerides occurred in 51.3%, phospho-lipids — in 26.9%, sterol esters — in 15.2%, and free aliphatic acids only in 6.6%, in relation to the total amounts of the fractions examined.

An increase in the glyceride contents in blood serum, noted in December, may express the mobilization of fat reserves to compensate the energy deficit during the spawning-season and during the wandering for spawning. A high content of phospho-lipids (compounds allowing fats to be assimilated regularly) in blood serum noted in June may prove the intensity of digestion processes in this period (Dominas 1963). A high content of free aliphatic acids in blood serum, noted in June, and a considerable individual oscillations may be related to the amounts of the food absorbed. Lovern (1951) informs that the fish reveals a highly active thyroid lipase, their digestion process is intense, and fats are absorbed, to be then deposited in an unchanged form.

Due to a considerable convergence of the results in both periods, the aliphatic acids will be described together.

Among saturated acids $C_{16:0}$ took an important place in the fractions of phospho-lipids (50.25% and 43.02%) during the periods examined. In the other fractions it always amounted to 10% and more. Acid $C_{18:0}$ was most frequently found in phospho-lipids and sterol esters (10–14%). In the other compounds it was from 1 to 14%. Among the aliphatic acids were investigated, those having 16 and 18 carbon atoms in chain prevail; in the case of glycerides, additionally also those with 22 carbon atoms (24.94% and 21.40%).

Total cholesterol. The average amount of the total cholesterol in blood serum of the bulltrout individuals was in June 381 mg in 100 ml, but during the artificial spawning-season — as much as 492 mg, this corresponding to an increase by 29.2%. Hypercholesterolemia, observed during the spawning-season, may be here of transport character, since as it is already known (Grundy and Griffin 1959), the estrogenes secreted in excess, circulate in blood in the form of various complexes with proteins.

The spawning may be considered here as a stress that changes the transformation of lipids by means of central nervous system.

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STUDY ON THERMAL ADAPTATION AND ON STIMULATION RATE OF THYROID GLAND IN CARP, TENCH AND TROUT

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ABSTRACT

The following parameters have been measured on carp, tench and trout within two temperature ranges (6–9 and 10°C, and 16–19 and 20°C): rectal measurement of body cavity and accumulation of intraperitionally injected radioiodine by the thyroid gland and by the whole body of fish. Moreover, determinations have been made of blood radioactivity and of quantity of radioiodine bounded with protein (PBI).

It has also been ascertained that both heat absorption and heat emission by the fish individuals examined depend, during the two-directional change in temperature of the environment ($10° \rightarrow 20° \rightarrow 10°C$), mainly upon the mass of their bodies. The greater is the mass of a fish, the longer is the period of its adaptation. As concerns dead fishes, which reveal already postmortal rigor, this process is little by little delayed. Accumulation of the intraperitionally injected radioiodine among the carp individuals kept within a higher temperature range is distinctly higher than that of the carp individuals from the lower range. Among the tench and trout individuals these differences are less visible. At higher temperatures all the species examined show that the release of hormonal iodine into the circulation of blood is more intense, this pointing to a dependence of the rate of metabolic processes in the thyroid tissue upon the thermal conditions of the environment.

INTRODUCTION

Investigaticns conducted by Suhrman (1955), Fontaine et al. (1955), Olivereau (1955a–c) or Houston (1962) point to an important and so far unexplained dependence of the state of thyroid gland stimulation upon the temperature of the environment, and the ability of thermal adaptation of fish, related to this phenomenon. This report deals with the thermal changes in carp, tench and trout bodies subjected to the fluctuating temperature of water environment ($10° \rightarrow 20° \rightarrow 10° C$). The same species have also been examined as to the accumulation and excretion of the intraperitionally injected iodine (^{131}I) in a temperature of 6–10°C and 16–20°C.

MATERIAL AND METHOD

The following fish species served as experimental material: two-year-old tench (*Tinca tinca* L.) — 32 specimens (among them 12 used for isotope exami-

nations); two-, and three-year-old trout (*Salmo gairdneri* Rich.) — 48 speci-
mens (among them 12 used for isotope examinations), and one-, two-, and
three-year-old carp (*Cyprinus carpio* L.) — 43 specimens (among them 6 used
for isotope examinations).

A. To determine the course of physical changes, fish individuals underwent
two-directional thermal changes of the environment ($10° \rightarrow 20° \rightarrow 10°$ C). After
a six-day adaptation of the fish individuals to the initial temperature (10°C),
they were brought to an aquarium, where water temperature was 20°C. Every
two minutes the temperature of their body cavity was rectally measured by
means cf a thermoelement of Leed and Northrup type (accuracy of measure-
ment — 0.1°C). The temperature measurement of fish was made under water
by introducing a sensing device of a measuring apparatus into the anus. The
temperature measurement was performed every 2 and then 5 minutes until
the body temperature became equal to that of the surrounding water masses.
In some minutes the fish individuals were again submerged in water, at a tem-
perature of 10°C, and similar reactal measurements were made at the same
time intervals as previously, till the equalization of body temperature with
that of the environment. An identical measurement cycle was then carried
out on the same individuals after the appearance of the postmortal rigor.

B. To investigate changes in the accumulation and excretion of radioiodine
among carp, tench and trout individuals subject to various temperatures,
a long-lasting cycle of experiments was executed. After a 4–8-day initial per-
iod during which the fish individuals adapted to a given temperature range
(I group — 6–9 or 10°C, II group — 16–19 or 20°C), the fish received initial
doses of NaI[131] (25 μ C per ind.) by the intraperitional injection.

Among all the individuals taken for the experiments, measurements of I[131]
accumulated in the thyroid gland were made, and distribution of this chemical
element in the entire body was determined according to the method described
above (ŁYSAK 1964). Such measurements, which allow us to plot "maps of io-
dine distribution", i.e. the so-called iodograms, were made during each of the-
se experiments carried out at the Agricultural College in Cracow, 2–3 times on
the same living fish individuals, anaesthetized, by means of urethane. On the
other hand, during the experiment carried out on carp in Great Britain, Torry
Research Station, Aberdeen, eight measurements were made of the iodograms,
during an experiment lasting 16 days.

Among all the fish individuals determination of absolute radioactivity of
blood and water environment was made, too, and the amounts of radioiodine,
bounded with protein in blood (PBI), were calculated according to the method
given by LYBECK (1957). All the fish individuals were under observation thro-
ughout a period of 8–16 days from the moment of the radioiodine injection.

RESULTS AND DISCUSSION

The results of the measurements of body cavity temperatures among the
carp, tench and trout individuals are graphically presented in Fig. 1A and B.
They demonstrate that the utmost heat absorption and heat emission in fish
takes place at the initial period after the change in water temperature, whe-
reas the time necessary to obtain a complete equalization of the body tempe-
rature with that of the environment, within the temperature range here exa-
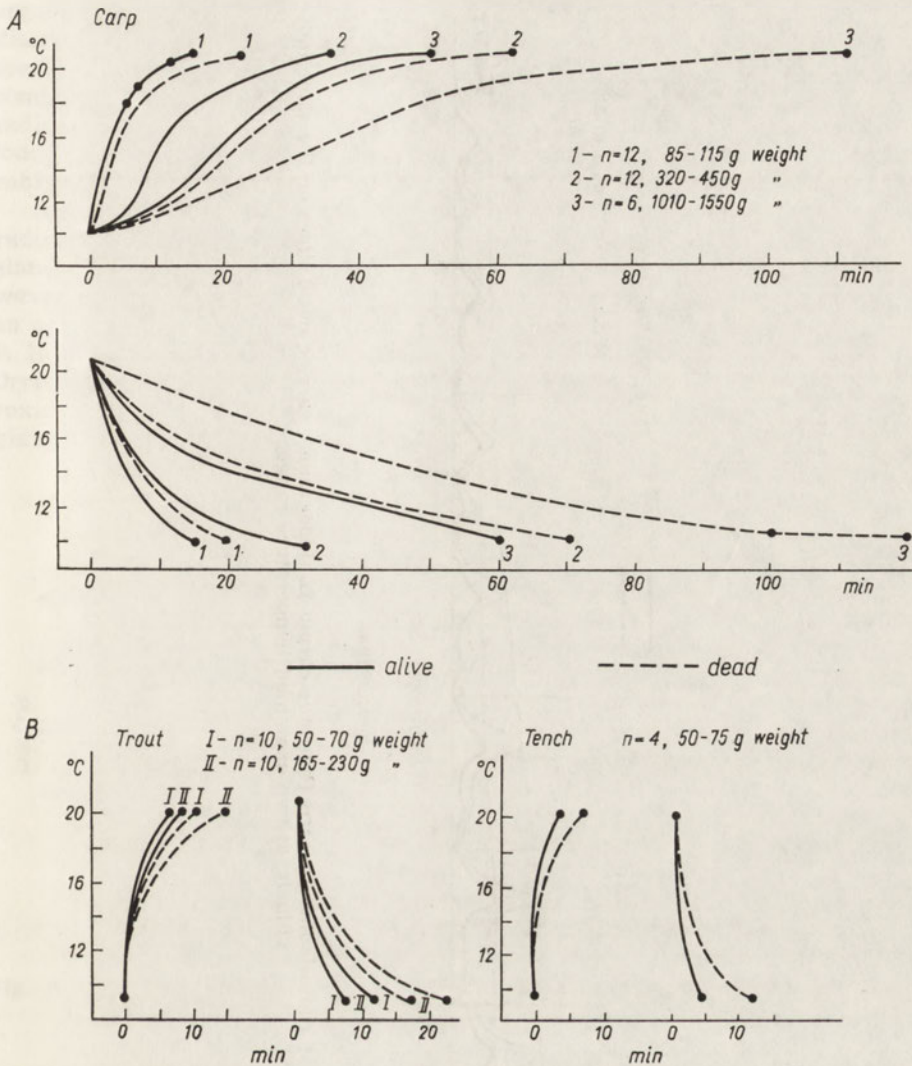
Fig. 1A — Course of temperature changes of carp body cavity at variable tempe-
rature of aquatic environment (10–20–10°C), 1 — one year old, 2 — two year old,
3 — three year old carp. B — Course of temperature changes of tench and rainbow
trout body cavity at variable temperature of aquatic environment (10–20–10°),
I — one year old, II — two year old trout

mined, depends upon the mass of fish body. No differences have been noted to
appear between the body cavity temperature and that of water temperature,
mainly due to a too low sensitivity of the measuring apparatus. According
to HALSBAND (1953), the body temperature of trout differs only by 0.012°C
from that of the water environment. After the appearance of postmortal
rigor, dead fish get hot and cool down slower than the same individuals
while alive. This is due to the elimination of the circulation of blood that, in
the case of heterothermal animals facilitates the heat exchange between the
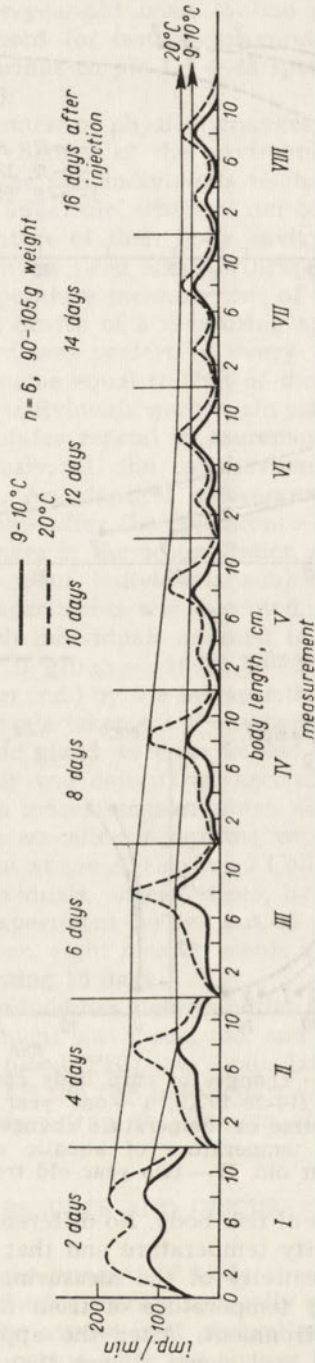
Fig. 2. Distribution curves of radio-iodine (iodograms) in carp *Cyprinus carpio* L. carried out 8 times on the same individuals, at two examined temperature ranges

organism and environment. The iodograms, which illustrate the radioiodine distribution in carp, are shown in Fig. 2. As compared with the other fish species, the thyroid tissue of carp is more scattered (ŁYSAK 1962) and, under conditions of rised water temperature, it distinctly reacts by increasing its radioiodine accumulation. As it may be seen on the diagram, the average iodograms for the carp individuals from a temperature of 9–10°C are considerably lower than those for carp of a higher temperature range (20°C).

An ability to accumulate radioiodine by thyroid gland, i.e. the so-called radioiodine uptake, represents a value analogous to the indicator of thyroid gland stimulation, known in human medicine. This indicator concerns, however, only the first stage of the physiological role of the thyroid gland in an organism, i.e. the ability to accumulate iodine from the circulation of blood. A linkage of the assimilated radioiodine with protein, their alteration into thyreoglobulin complexes, and a liberation of hormones, in the form of thyroxin and triiodothyronin, into blood, are the next stage of the activity of this gland. This process appears in fish, several days after the injection. It results
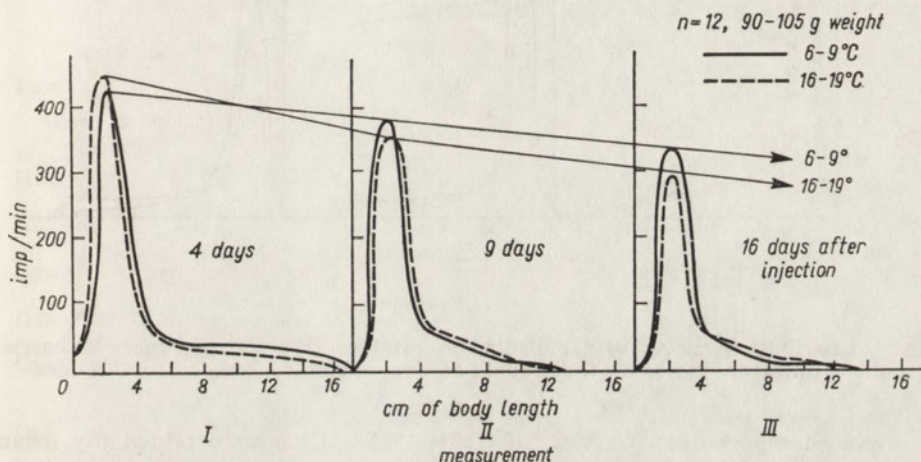
Fig. 3. Distribution curves of radioiodine in tench (*Tinca tinca* L.) carried out 3 times on the same individuals, at two examined temperature ranges

in a decrease in ^{131}I accumulated previously in the thyroid tissue. In Fig. 2 the peaks of the iodograms which correspond to the thyroid tissue are connected, in both temperature ranges, by a straight line. The inclination degree of these lines, different in these temperature ranges, reflects the intensity of iodine transfer in hormonal form into blood. The inclination of this line at a temperature of 20°C is more abrupt than that at the temperature range of 9–10°C. This points to a more intense production of hormones in thyroid tissue by the first carp group, at higher temperature.

As far as tench is concerned the effect of temperature on the intensity of the radioiodine accumulation in the thyroid gland was, during the 16-day period of experiments, considerably lesser than that in the case of carp (Fig. 3). At a temperature of 6–9°C, the tench individuals revealed only a slightly lower degree of accumulation, as compared with those kept at a temperature

16–19°C. A comparison of the straight lines which connect the peaks of the iodograms, points to a considerably more intense elimination of hormonal iodine from the thyroid gland, at the higher temperature range, during both the ninth and sixteenth days after the injection, as compared with the fourth day. It has also been ascertained that four days after the injection at the lower temperature (6–9°C) the thyroid gland of trout individuals shows somewhat lesser ability to accumulate iodine (Fig. 4), in relation to the fish individuals examined at higher temperatures (16–19°C). Like in the case of carp and tench individuals, the comparison of the inclination of the lines that connect the thyroid peaks of iodograms in both temperature ranges, demonstrates that among the trout individuals the elimination of hormonal iodine is more intense
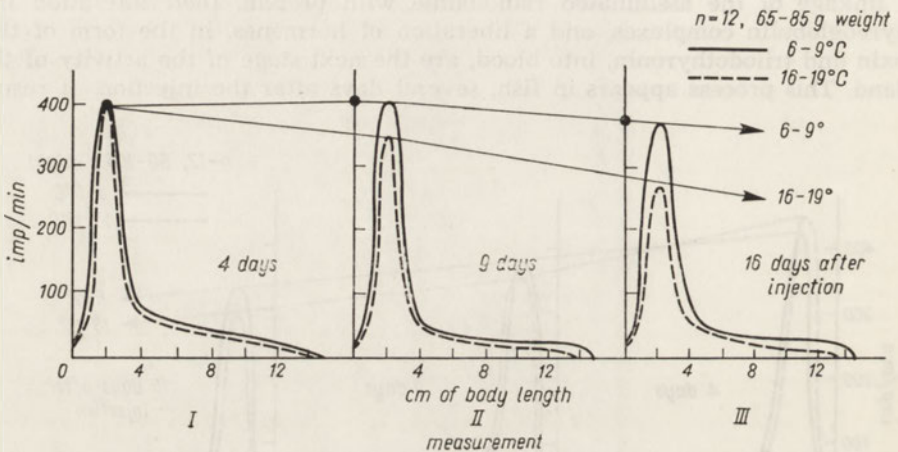
Fig. 4. Distribution curves of radioiodine in rainbow trout, *S. gairdneri* R. carried out 3 times on the same individuals at two examined temperature ranges

at higher temperatures. OLIVEREAU (1954, 1955a–c) has ascertained (by means of histologic methods and by measurements of uptake) that the stimulation rate of thyroid gland of this species is, at the lower temperature, somewhat higher, but the examinations were carried out in a four-day period only, on the fish individuals kept at the temperature ranges below (9–12°C) and above (20–23°C) the thermal optimum of this species. On the other hand, the lower range, amounting to 6–9°C (i.e. 7.5°C on the average), applied during the research discussed at present, is found to be more deviated from the optimum, whereas the upper one, which amounts to 16–19°C (i.e. 17.5 on the average) is almost equal to this value. This problem calls for an additional study, mainly due to the seasonal variations in the thyroid gland activity described, as concerns this species, by SWIFT (1955, 1959).

It may be inferred from the measurements of the activity of the water environment that all the fish species examined remove their radioiodine excess into the water environment in the same way. An the higher temperature ranges, the fish eliminates more iodine than that at the lower temperatures. A reduction in temperature by 10°C is responsible for a considerable decrease in rate of this process.

CONCLUSIONS

1. Both absorption and emission of heat by carp, tench and trout individuals during the two-directional change in the environment temperature $(10° \to 20° \to 10°C)$ mainly depend upon the mass of their body. The greater is the mass of fish, the longer is its adaptation period. In the case of dead fish individuals characterized by the appearance of postmortal rigor, further retardation of this process proceeds.

2. The uptake of the intraperitioneally injected radioiodine in the carp individuals kept at the higher temperature range is markedly higher, as compared with those kept at the lower one. Among the tench and trout individuals these differences are lesser. On the other hand, all the species examined after 8–16 days after the injection show that at a higher temperature the elimination of hormonal iodine into blood is considerable and more intense, this proving the dependence of the rate of changes in the thyroid tissue upon the thermal conditions of the environment.

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RESPIRATORY SURFACES OF WHITE-BLOODED FISH
CHAENICHTHYS RUGOSUS REGAN (PERCIFORMES)

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ABSTRACT

The vascularization of gill, skin and lining of the oral cavity of the specimen *Ch. rugosus* from the environs of Kerguelen island were investigated. The branchial laminae are small but well vascularized; the surface of the capillary is 80% of the lamina surface. The skin is also well vascularized: 23–45 mm long and 1.13–2.20 mm² of capillary surface per 1 mm² of skin. The surface of dermal capillaries together with the capillaries of oral cavity are 3 times greater than the surface of branchial capillaries. The possible significance of skin vascularization in the gas exchange of this fish is discussed.

Lack of erythrocytes as well as haemoglobin or other respiratory pigment in the blood of Antarctic fishes from the Chaenichthyidae family (Ruud 1954, 1958, Martzinkevitch 1961 and others) is a curiosity among vertebrates. These fishes are adapted to life in waters of a very low temperature, about — 2°C (Wohlschlag 1963, Andriashev 1965). The gas exchange of these fishes has not been investigated yet. These fishes are quite often very big, even 67 cm long (Andriashev 1965), and their body proportions are very specific (Table I, Fig. 1).

As the gas exchange between the blood and the medium, in the instance
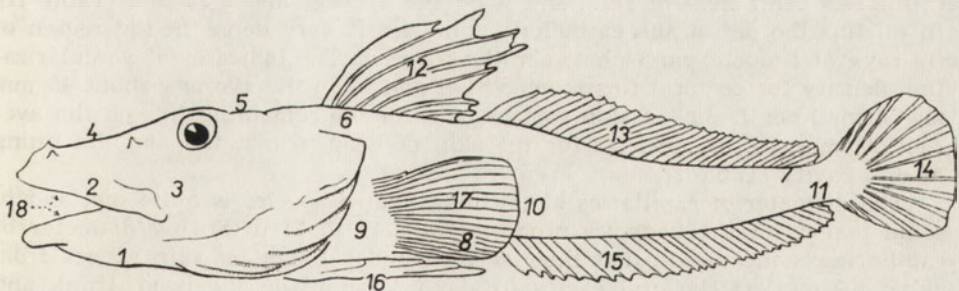
Fig. 1. *Chaenichthys rugosus* Regan. The regions, in which the density of skin vascularization was measured, are marked with numerals

Table I. The body surface of *Chaenichthys rugosus* Regan

	A	
Head		25 370
Trunk and tail		27 102
	total	52 472
	B	
Pectoral fins		10 632
Abdominal fins		9 448
Dorsal fin I		4 620
Dorsal fin II		4 850
Anal fin		5 136
Caudal fin		3 608
Total body	total	38 294
surface (A+B)		90 766
	C	
Oral cavity		14 560
Surface of body and oral		
cavity — total (A+B+C)		105 326 mm²

of these fishes, takes place probably by means of ordinary diffusion, one should expect strong vascularization of organs used for respiratory purposes and first of all those organs that have a direct contact with water medium, i.e. skin, oral cavity and gills. And this is the subject of this paper.

The extent to which the respiratory surfaces are vascularized was examined on one individual of *Chaenichthys rugosus* (♀), measuring 375 mm and weighing 450 g. The blood-vessels of this specimen were filled with black drawing ink. This specimen was caught in January 1966, in the neighbourhood of Kerguelen island, during the cruise of the ship "Sovetskaya Ukraina". The investigations were carried out and the obtained results described in an analogical way as at similar analysis of gills (BYCZKOWSKA-SMYK, 1957–1962) and skin (JAKUBOWSKI 1958–1963) of fish having a typical blood morphology.

Skin capillaries, taken into consideration at these calculations are in the proper skin just under the epidermis, where they form a capillary net of an irregularly shaped meshes. The density of sub-epithelial capillary net in different places of the head and trunk is similar, and is expressed by the length of capillaries per 1 mm² of skin, and is on the average about 23 mm (Table II). In all fins the net of sub-epithelial capillaries is very dense in the region of fin rays, and much sparcer between the fin rays. The indicator of vascularization density for pectoral fins is very high and is on the average about 45 mm (36–54 mm) per 1 mm² of skin surface, and for the remaining fins on the average 23 mm, i.e. as much as for the skin of head, trunk, tail and the lining of oral cavity (Table II).

The diameter of capillaries of the investigated species is quite big, and in some regions of the body its range is from 13 to 21 μ. So big diameter of capillaries is the reason that their surface under 1 mm² of skin ranges from about 0.9 mm² in the oral cavity to about 1.3 mm² on the head, trunk and tail, and up to 2.2 mm² on pectoral fins (Table I).

The capillaries of the lining of mouth cavity were taken into consideration

because of the large size of the mouth of the investigated species. The surface of the mouth cavity is in this case almost 17% of other investigated surfaces of the fish's body. The participation of fins in the total body surface is big. They cover 36% of all body surfaces, which are in touch with water (without gills), or 42%, if the surface of mouth cavity is not taken into consideration. The surface of all fins together with the surface of mouth cavity is equal to the surface of head, tail and trunk altogether (Table I).

Table II. Vascularization of different body regions of *Chaenichthys rugosus* Regan

Investigated body region	Diameter of capillaries (μ)	Capillaries in mm² of skin			Capillaries per 1 g of body weight		
		Length		Surface (mm²)	Length (mm)	Surface (mm²)	Capacity (mm³)
		mm	average				
Mandible	20.8	23.65					
Jaw	17.3	24.25					
Chin	20.6	20.01					
Top of the head	17.7	26.42					
Top of the head	17.5	27.06					
Back of trunk	17.2	26.82	23.0				
Back of tail	16.2	25.03					
Anus	17.8	23.83					
Pectoral girdle	15.0	17.10					
Side of the body (above the anus)	18.5	20.00					
Side of the tail	16.1	23.98					
Head, trunk and tail (together)	17.7		23.0	1.28	2682	149.1	0.660
Dorsal fin I							
Dorsal fin II	14.8	23.04[a]					
Caudal fin			23.0	1.13			
Anal fin	15.2	24.76[b]					
Abdominal fin	16.8	20.84					
Pectoral fins	15.6	44.93[c]	45.0	2.20			
All fins (total)	15.6				2699		
Total body surface regions 1—17					5381	270.4	1.028
Oral cavity	12.8	22.77	23.0	0.92	744		
Total (regions 1—18)					6125	322.5	0.788

a about 26 mm above the rays, 20 mm between rays.
b 31 and 19 respectively.
c 54 and 36 respectively.

All capillaries of skin and mouth cavity were calculated into units of individual's body weight. These calculations show that there is as much sub-epithelial capillaries in the skin of fins as in that of trunk, head and tail altogether. The capillaries of the lining of mouth cavity of *Ch. rugosus* cannot be ignored as they are 1/7 (744 mm/g) in relation to all other (5381 mm/g) subepithelial capillaries (Table I).

Macroscopically the gills of *Ch. rugosus* resemble the gills of pike. The

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branchial arches are elongated, elastic and of delicate structure. The gill-
rakers are poorly developed. In case of *Ch. rugosus* they do not have the
shape of longer or shorter appendixes, as it is usually in the majority of fishes.
They have a form of rounded bone shields. These shields are flat, equiped with
short, stiff scales. The height of such shield is about 1 mm, and the length of
respective scales is smaller. On one branchial arch there are from several (5)
to more than ten (13) shields. They are usually along the middle line of bran-
chial arch, however, especially on the I and II arch smaller additional shields
are found on the sides of main shields. On one specimen, of similar size, and
also *Ch. rugosus*, which was not used in the investigations as there were no
data on its body weight, the arrangement of shields was different. Namely,
these shields run in two lines along the arch and are slightly off the middle
line of the arch to the sides but are not in front of each other but alternately.
The branchial lamellae form holobranchium and are rather of average length.
Only some of them attain the maximum length of 13 mm, while the majority
of lamellae is 6–10 cm long. The largest amount of branchial lamellae may be
found on the I arch, and the least on the IV arch. Slight assymetry was noticed
between the arches of the right and left side of the body. The length of right
branchial arches, measured at the lamellae base, is 96, 82, 74 and 59 mm, and
of left arches — 92, 78, 76 and 59 mm. On the I, II and IV right arch there is
some more branchial lamellae than on the corresponding arches on the left
side of the body. Only on the III right arch there is less lamellae than on the
left one. Taking into consideraticn the total length cf branchial lamellae, the
lamellae of the I and II right arch measured together are longer than the I and
second left ones. On the other hand the lamellae of the III and IV left arch are
longer than those on the right side. And so, the final total length of all la-
mellae of right arches is almost identical as that of the left arches.

On 1 mm of branchial lamella there is on the average 24 laminae. On all
branchial arches in one individual 252, 312 laminae were counted.

Vascularization of branchial lamella and laminae is the same as of other
teleost fishes. The shape of single lamina is typical.

The average total surface of one side of branchial lamina is 0.12 mm², out
of which the blood vessels i.e. respiratory surface or the surface of gas exchan-
ge covers 0.0957 mm i.e. abcut 80⁰/o. The total bilateral surface of all branchial
lamine of the examined specimen is 60,555 mm², and the respiratory surface
(bilateral) — 48,293 mm². 107 mm² of the gill's respiratory surface falls per 1 g
of body weight, which can be presented as a square with sides 10.35 mm long.

The extent of vascularization of different respiratory surfaces may be de-
termined by two indicators: 1) indicator of the vascularizaticn density of
a determined surface unit of an organ and 2) vascularization indicator calcu-
lated per unit of animal's body weight. Both indicators may be expressed by
length, surface and capacity of sub-epithelial capillaries, but the former is for
vessels e.g. 1 mm² of organ surface, the latter — all the remaining vessels of
the organ (or organs) calculating per 1 g of body weight. Vascularization in-
dicator per unit of body weight determines the participation of investigated
organ in the total gas exchange, i.e. the evidence of its respiratory value for
the organism. The conclusions taken from morphological data are approxima-
te and require a comparison with the results of physiological and ecological
investigations with consideration to such factors as e.g. Hb contents in the
blood, its affinity to oxygen, the mode of life spieces etc. Comparison of mor-

phological and physiological data of different fish species would help to draw conclusions of a wider biological significance in general.

The presence of sub-epithelial capillaries in 1 mm² of skin, 23 mm long, and on trunk fins even 45 mm on the average, places *Chaenichthys rugosus* among the fishes having rich skin vascularization. As far as the density of capillary net in skin is concerned, *Ch. rugosus* is slightly behind the pond-loach, is equal to carp and is definitely above the eel, burbot and other species that have been already examined from this point of view (JAKUBOWSKI 1958–1963, KACZMARSKI 1966, TYSZKIEWICZ 1969). Apart from that the dermal sub-epithelial capillaries in *Ch. rugosus* have on the average 17 μ of diameter, while in other fishes they are usually on the average 10 μ. This has a great effect on the increase of surface and capacity of capillaries.

Table III. Comparison of respiratory surfaces in gills and skin

Species	Body weight in g	Surface of capillaries per 1 g of body weight in mm²		Proportion of branchial vessels to dermal ones
		gills	skin	
Esox lucius	195–222	1593	52 75*	31 : 1 21 : 1*
Misgurnus fossilis	32–55	480	170	3 : 1
Anguilla anguilla	55–98	990	112	9 : 1
Lota lota	45–98	639	108	6 : 1
Acerina cernua	14–38	904	85 150*	11 : 1 6 : 1*
Chaenichthys rugosus	450	107	149 270* 322**	0.72 : 1 0.4 : 1* 0.33 : 1**
Zoarces viviparus	75–210	475	52	9 : 1
Cottus gobio	11–44	301	151	2 : 1
Platichthys flesus	29–99	801	75	11 : 1

* Together with fin capillaries.
** Together with fin and oral cavity capillaries.

It is peculiar that the surface of sub-epithelial capillaries of *Ch. rugosus* in 1 mm² of skin is 1.13–2.20 mm², depending on the part of body (Table II). Till now it has not been found either in fishes (JAKUBOWSKI 1958–1963) or in amphibians (CZOPEK 1965a, b) that the surface of sub-epithelial dermal capillaries would be equal or greater than the body surface.

From the point of skin vascularization calculated per unit of body weight *Ch. rugosus* does not differ from the majority of fishes (Table III). However the investigated specimen is considerably heavier than the body weight of the fish species that have been alread yexamined. Therefore it can be assumed that in small *Ch. rugosus* individuals the vascularization indicator per 1 g of body weight would be considerably higher than that of pond-loach of a similar body weight. This assumption is based on the already stated fact (JAKUBOWSKI 1958–1963) that the density of capillary net in the skin of individuals of different size but the same species is practically identical also on slower increment of body surface than its weight. Judging only by the surface of dermal capillaries *Ch. rugosus* deserves its leading place in the table.

The size of the respiratory surface cf gills is determined by such factors as the length of branchial arches, number and total length of branchial lamellae, density of laminae on lamellae, the size of lamina itself and the density of vascular net on it.

The laminae of *Ch. rugosus* are small. Smaller than that were found in *Acipenser stellatus,* almost the same in *Zoarces viviparus* (OLIVA 1960). In other fishes the laminae were bigger. But the density of vascular net is quite considerable in *Ch. rugosus.* In the majority of compared fishes the blood vessels cover 62–72% of the total surface of lamina, in *Ch. rugosus* 80% and only *Engraulis encrassicholus* is on the same level (80%). The character of vascular net in the lamina is the same as in other fishes.

An important factor determining the size of respiratory surface of gills is the number of branchial lamina falling per 1 mm of lamella length. The size does not change together with the growth of individual and therefore can be compared in individuals of different size. Among the species compared *Ophicephalus striatus* (SAXENA 1962) has the smallest number of laminae i.e. 16 on 1 mm length of the lamella, *Anabas testudineus* has 23 (SAXENA 1962), and *Acipenser stellatus, Tinca tinca, Misgurnus fossilis, Lota lota* (BYCZKOW-SKA-SMYK 1959, 1962) and just now examined *Ch. rugosus* — all have 24 laminae. Other species have the laminae more densely arranged, usually there are 30–36 laminae per 1 mm. *Alosa kessleri pontica* (CZOŁOWSKA 1965) has very much laminae i.e. 60 per 1 mm, *Engraulis encrassicholus* (ROMANIEC, unpublished data) has 65 and *Trachurus trachurus* (NOWCGRODZKA 1963) has 72 laminae per 1 mm (Table IV).

The proportion of respiratory surface to the body weight becomes less

Table IV. Comparison of the respiratory surface in gills of various species

Species	Body weight (g)	Amount of branchial laminae on 1 mm of lamella length	Surface of 1 lamina mm$^2 \cdot 10^{-3}$	The branchial lamina surface occupied by vessels	Respiratory surface per 1g of body weight in mm^2
Acipenser stellatus	66–108	24	180	73	264
Alosa kessleri pontica	25– 78	60	258	75	3521
Engraulis encrassicholus	15– 18	65	221	80	2515
Salmo irideus	45– 70	30	348	71	1319
Salmo irideus	130–160	30	436	71	989
Esox lucius	200–300	30	475	65	1432
Tinca tinca	100–180	24	505	68	1078
Blicca bjoerkna	40– 70	36	432	67	1641
Chondrostoma nasus	100–220	28	421	68	684
Labeo rohita	26–108	33			1090
Misgurnus fossilis	30– 55	24	342	64	527
Anguilla anguilla	55– 99	30	487	67	990
Odontogadus merlangus	16– 28	43	210	76	1595
Lota lota	50– 98	24	312	62	639
Lucioperca lucioperca	40–150	30	485	67	1800
Perca fluviatilis	50–100	36	461	72	1675
Acerina cernua	10– 45	30	202	62	1032
Chaenichthys rugosus	450	24	120	80	107
Trachurus trachurus	20– 35	72	45	70	818
Zoarces viviparus	75–210	31	128	75	475
Cottus gobio	11– 44	30	318	69	301
Anabas testudineus	38– 65	23			155
Ophicephalus striatus	49– 78	16			265
Platichthys platessa	100–170	28	530	63	676
Platichthys flesus	29– 99	36	240	67	801

advantageous as the individual grows (Fig. 2). The investigated specimen of *Ch. rugosus* was big, when compared with other species, and that is why the calculations show that per 1 g of body weight falls a relatively small respiratory surface of gills. These values would be higher if the investigated individual was small. But despite all this *Ch. rugosus* has a rather small respiratory surface. These values can be only compared among individuals of a similar shape, size and age.
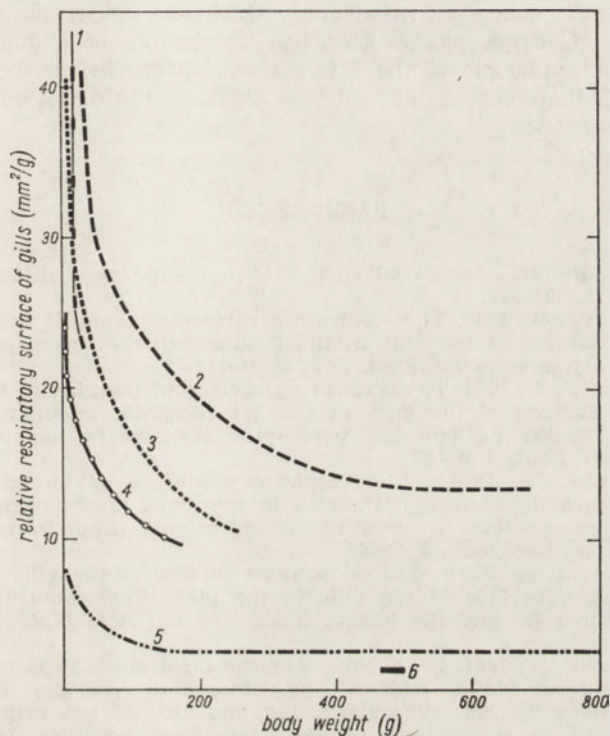
Fig. 2. Size respiratory surface of gills per unit of body weight in individuals of different size. 1 — Alosa, 2 — Cyprinus, 3 — Carassius, 4 — Salmo, 5 — Micropterus, 6 — Chaenichthys

The size of the surfaces of branchial and dermal capillaries as calculated per 1 g of body weight are different in each species (Table III). In fishes having in blood erythrocytes the proportion of these surfaces is always two times in favour of gills and sometimes even twenty or thirty times. In *Ch. rogosus*, in the blood of which the respiratory pigment is practically lacking, the surface of branchial capillaries is smaller than that of dermal capillaries: in proportion to dermal capillaries of the head, body and tail 1.4 times, after the addition of fin capillaries 2.5 times, and 3 times, when adding the capillaries of oral cavity. In case of the white-blooded fish *Ch. rugosus*, similar respiratory dependences should be expected between gills and skin also in direct measurements of the participation of each respiratory surface in the total gas exchange.

On the account of observations on paraffin sections of the skin of white-blooded fish *Chaenocephalus aceratus*, WALVIG (1960) comes to the conclusion that the skin of this species is well vascularized. Finding the presence of a greater amount of wide blood vessels in the abdominal fins he ascribes them a special significance in the gas exchange. Our observations, which result from direct measurements of sub-epidermal capillaries in *Chaenichthys rugosus* show that the pectoral fins are most abundantly vascularized, while the abdominal fins are most poorly vascularized. Apart from that the massive abdominal fins are covered with strongly thickened epidermis, which WALVIG also noticed in *Chaenocephalus aceratus*. Thickening of abdominal fins and especially their epidermis of these two slow bottom fishes should be rather connected with their supporting function. Also on the distal edge of anal fin epidermis is thickened.

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J. Kucias

ESTIMATION OF CELL METABOLISM OF AQUATIC ANIMALS BY MICROSCOPE MEASUREMENTS

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ABSTRACT

The correlation between the metabolic activity of the cells and the nucleus size as well as its plasma-nucleus ratio allows the estimation of the reaction of the organism to environmental factors on the level of the cell metabolism. Basing on the Fick equation concerning the velocity of diffusion the quantity of oxygen utilized by the cell in the conditions in which it operates in the organism, can be calculated. In the lecture the author introduces technical details of the method and discussed its reliability, basing on examples of aquatic animals (Xenopus, Ambystoma).

Between the cell metabolism and its morphological parameters, such as nucleus size and nucleoplasmic ratio, a relation exists, caused by physic--chemical conditions of biochemical processes. During the respiration, in cells are formed zones of minimum concentration of oxygen and of maximum saturation with CO_2. Thus, the cell metabolism considerably depends upon the free diffusion of these two gases. This is related to the size and shape of both cell and nucleus. Since the principles of the method and numerous examples and references described in this paper have already been published in the Biologisches Zentralblatt (Kucias 1966, 1967 a–d), the author restricts the problem to a concise description of this method, giving its slightly simplified version only.

The estimation of the metabolism consists of three stages: 1) preparation of histological specimens; 2) measurements of nucleus size and of nucleoplasmic ratio; 3) calculation of oxygen consumed by a cell. As a rule, measured may be each histological specimen that allows the investigator to classify also the nucleusless fragments of cytoplasm. Thus, in most cases it is enough only to dye the preparations by means of hematoxiline/eosine. On account of a considerable shrinkage caused by alcohol fixatives, water fixatives are recommended.

Point grid, necessary to make measurements, may be prepared in the following way:

The 22 cm long parallel lines are drawn on a sheet of paper, 8.6 mm apart. On each line are marked sections, 10 mm in length. The first point situated on

the upper line is connected with the sixth point on the lower line, the second point with the seventh point, a.s.o. The same must be repeated with the points calculated from the opposite side. By connecting the upper sixth point with the lower sixth point, and the upper sixteenth point with the lower sixteenth point, we obtain a rectangle, the area of which must be then subdivided into equilateral triangles (Fig. 1). The grid, drawn in this way on a sheet of paper, is then provisionally fastened to a black cardboard sheet, and perforated at points where the lines of the rectangle intersect. After-
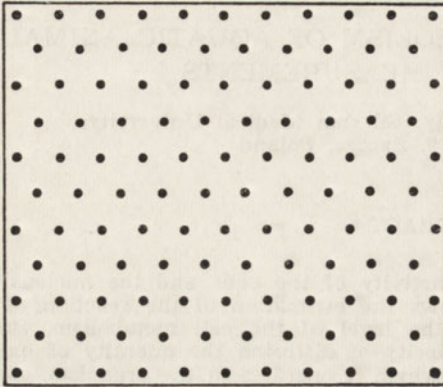
Fig. 1. Point grid for measuring nucleus size and nucleoplasmic ratio

wards, the cardboard sheet with the apertures is underlain with a tracing paper, and illuminated from behind. After setting in the drawing eyepiece with drawing aperture directed forwards, this device is placed behind the microscope in a way allowing the whole grid of the illuminated points to be visible in the field of view of the microscope. The distance between the grid and eyepiece should amount to about 25 cm. By means of micrometric plate set under the microscope, instead of a preparation, we measure then the distance between the points (-a) by means of an immersion lens ($\times$90). If the grid-microscope system undergoes disturbance, the measurement must be repeated.

After replacing the micrometric plate for a preparation we point a fragment of the specimen at a venture, and by means of micrometer screw we bring it into focus to obtain sharp structures visible in the whole field of view. Then we stop the operation with the micrometer screw until we end the measurements in the field of view. At first we count the number of nuclei (N_0) found to appear within the grid. We count also these which touch the right and the lower margins of the grid from the outside. However, nuclei that touch the upper and the left margins of the grid are not taken into account, even if they rest inside. All cut fragments are considered to be nuclei, as well. The counting of hits at the sharply visible parts of the nucleus (N_f) is the next step in our procedure. Points that contact with the left and the upper margins of the structures observed are not taken into account. The number of hits at a cell may more practically be estimated by counting points that fall outside the cells (both the left and the upper margins of the grid are not taken into account). By subtracting this number from 100, we obtain the amount of hits at a cell (C_f). To obtain a number of nuclei (N_0)

greater than 500, an adequately great amount of fields of view should be examined. With the increase in this number, we also increase the sensitivity of the method applied. Then, above the grid we place a sheet of graph paper and illuminate it in front. By means of this grid projected through the drawing eyepiece on the field of view measured the lengths of both long and short axes of each nuclear structure found to appear in the field of view. The graph paper allows us to make measurements without moving preparations, thus without using micrometer screw. Dividing the values for long axis by those for short axis we obtain a value of eccentricity of the nuclei (ε'). Measurements of only 20–30 nuclei are adequate to establish the average eccentricity here. The data obtained are shown in the Table I of measurements.

Table I

Number of nuclei	Number of hits at nuclei	Number of hits at cells	Average section of nucleus	Average radius of nucleus	Nucleoplasmic ratio	Eccentricity of nucleus
N_0	N_t	C_t	$f_{mk} = 0.86a^2 \cdot \dfrac{N_t}{N_0}$	$\bar{r}' = 0.564 \cdot \sqrt{f'_{mk}}$	$H'_p = \dfrac{C_t}{N_t} - 1$	ε'

These values are additionally charged with an error, which is related to the depth of focus of the microscope picture (T). For a young person of twenty five the value T amounts to about 0.6 μ, for a person of forty, in turn, this value is 0.55–0.5 μ (an objective $\times 90$ having an aperture 1.25 and a drawing eyepiece $\times 15$).

Dividing the depth of focus T by the average radius of nucleus $\bar{r}$, we obtain $S = \dfrac{T}{\bar{r}'}$. A correction for the parameters obtained may be read off on the nomogram attached (Fig. 2). On the left side of the nomogram are found initial data that should be connected by a straight line with a respective value S. The production of this line points to the values in demand, on the right scale. The way of making such a correction is explained by a specific example. The following are the results obtained for a hepatic cell of *Ambystoma tigrinum*:

$$f'_{mk} = 69\,\mu^2; \quad \bar{r}' = 4.7\,\mu; \quad \varepsilon' = 1.26; \quad H'_p = 6.7.$$

Thus S amounts to:

$$\frac{T}{\bar{r}'} = \frac{0.6\,\mu}{4.7\,\mu} = 0.13.$$

The values S for the fusiform nuclei are marked with S^s, those for the lenticular nuclei — by S^l. The nomogram gives the values for the lenticular nuclei, in the case of an ordered system, which may be encountered in cross sections, for example through epidermis. In this case ε' is equal to the actual value of eccentricity ε. The corrections for the fusiform nuclei concern only the chance arrangement of the long axis, observed to occur in the parenchyma organs. Thus we find $\varepsilon' = 1.26$ on the left scale, and then we connect this point
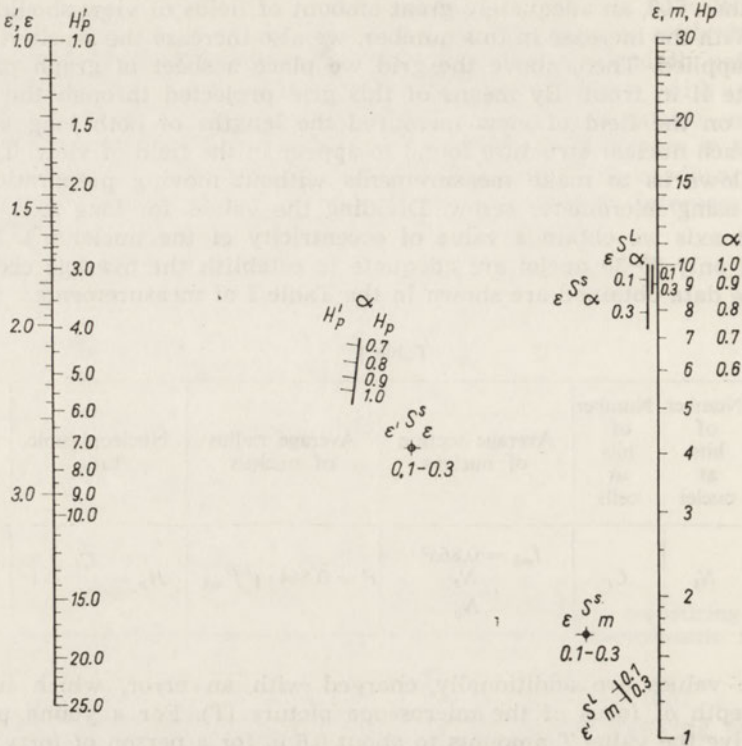
Fig. 2. Nomogram for correction of measurements

through $\varepsilon'^{S^s}\varepsilon$ with the right scale of the nomogram and read off the actual value of eccentricity $\varepsilon = 1.51$. Afterwards, we connect $\varepsilon' = 1.26$ through $\varepsilon'^{S^s}m$, and read off the value by which we multiply the measurement of the nucleus radius, i.e. $m = 1.2$. Thus, the average radius amounts to 5.6 ($\bar{r} = 5.6$). Connecting $\varepsilon = 1.51$ through $\varepsilon^{S^s}\alpha$ we obtain a value $\alpha = 0.92$, necessary to make the correlation cf the value of the nucleoplasmic ratio. Finally, the line running from $H'_p = 6.7$ through $H'^{\alpha}_p H_p = 0.9$ gives us the actual nucleoplasmic ratio $H_p = 7.2$.

By substituting the values obtained for $\bar{r}$, ε and H_p in the properly converted Fick's formula for free diffusion, we obtain the values of the oxygen consumed by a cell in 1 min (KUCIAS 1967 a–d):

$$\frac{dM}{dt} = FD\frac{dc}{l} = 4.18\,\bar{r}(\varepsilon+2)\sqrt[3]{\frac{H_p+1}{\varepsilon}} \cdot Dc\left(\frac{e^z-1}{e^z}\right)$$

for the fusiform nuclei, or

$$4.18\,\bar{r}(2\varepsilon+1)\sqrt[3]{\frac{H_p+1}{\varepsilon^2}} \cdot Dc\left(\frac{e^z-1}{e^z}\right)$$

for the lenticular nuclei.

D = diffusion coefficient, c = oxygen concentration in the cell environment, $z = (1+q) \ln H_p$, q = reciprocal of respiratory quotient. $\left(\dfrac{e^z-1}{e^z}\right)$ determines the decrease in oxygen concentration inside a cell. At the respiratory quotient amounting to 0.84 it takes the following values:

H_p	5	7	10	15	20	25
$\dfrac{e^z-1}{e^z}$	0.97	0.99	0.99	1.00	1.00	1.00

There are some difficulties in obtaining exact values of the diffusion coefficient.

1) At a temperature of 20°C the diffusion coefficient for oxygen in water amounts to $D = 2 \cdot 10^{-5}$ cm²sec⁻¹ (Prosser and Brown 1962). Applying the formulae given for a tissue, the oxygen consumption of which is known (Kucias 1967b), we may expect that under the poikilothermic conditions its values amount to about $1.15 \cdot 10^{-7}$ cm²min⁻¹.

2) For the embrional tissue of an axolotl Løvtrup (1965) gives $D = 4.8 \cdot 10^{-6}$ cm²sec⁻¹. If the oxygen concentration is equal to that of venous blood, i.e. to 0.11%, the following values may be obtained for the hepatic cell of an axolotl:

$$\frac{dM}{dt} = 4.18 \cdot 5.6 \cdot 10^{-4} \, \text{cm} \, (1.51+2) \sqrt[3]{\frac{7.2+1}{1.51}} \cdot 1.15 \cdot 10^{-7} \, \text{cm}^2 \times$$

$$\times \text{min}^{-1} \cdot 0.0011 \cdot 1.00 = 1.65 \cdot 10^{-12} \, \text{cm}^3 \, \text{min}^{-1} \, \text{oxygen}.$$

The whole operation connected with the multiplying and extracting the cubic root may, with an adequate precision, be performed by means of a slide rule. Knowing the dry weight of a cell, or even that determined only by mans of an interference microscope, we may calculate QO_2, dividing the oxygen consumption of the cell by its dry mass. In this way, for a cell of an axolotl

$$QO_2 = 0.4 \, \text{ml} \cdot \text{mg}^{-1} \cdot \text{hr}^{-1}.$$

It appears that the advantages of the method here considered consist not only in a fact which allows the oxygen consumption by a cell under normal physiological conditions to be calculated approximately, but that it permits us in any case to ascertain also the increase of the nucleus and of the nucleoplasmic ratio, as well as to determine the activation of metabolism. If, and to what extent, the other factors, as for example hydratation, change the cell parameters is being now an object of study. On the basis of the literature data (vide papers cited) we may say that such an influence — if any exists — is not considerable here. In the examinations of the aquatic animals the saturation of cell environment with oxygen may be very important. On the other hand, if we investigate a given factor, in which the parameters of an experiment are checked, and if we try to estimate only the intensity of change in metabolism, the exact knowledge of the oxygen concentration is superfluous. If, however, we aim at comparing the individuals of various biotopes or species, the omission of the oxygen concentration in water may lead to some erroneous conclusions. However, considering a markedly greater amount

of errors of the other methods applied in determining the cell metabolism we may assume that the method discussed in this paper is — mainly due to its simplicity — worthy of being considered.

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CONTENTS OF LIPIDS IN RESTING STAGES OF COPEPODA, CYCLOPOIDA

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ABSTRACT

5162 specimens of copepodites IV and V of *Cyclops bohater* Koźm., *Cyclops vicinus vicinus* Ulj., and *Cyclops vicinus kikuchii* Smirn. have been examined. At the time of the examinations these forms were in resting stage and occurred in the bottom sediments of an eutrophic basin characterized by the presence of sulphuretted hydrogen. Differences in the amounts of lipids were investigated at the beginning, in the middle and towards the end of the resting stage. At the beginning the amounts of lipids were as much as 20.3% (*C. bohater*), 9.9% (*C. v. vicinus*) and 6.4% (*C. v. kikuchii*) of dry weight. In the late resting stage period, the amounts of lipids of the copepodites *C. v. kikuchii* increased two times, whereas among the other species these amounts varied insignificantly only.

INTRODUCTION

The purpose of this study was to ascertain some changes in the amounts of lipids found to occur during the resting stage of Copepoda, Cyclopoida. The results of determination of lipids, presented in Table I, concern two species and one variety of the genus Cyclops, i.e. *Cyclops bohater* Koźm., *Cyclops vicinus vicinus* Ulj., and *Cyclops vicinus kikuchii* Smirn.

MATERIAL

The species mentioned above come from a clay-pit, an eutrophic basin in Warsaw. The same species are found to live in the eutrophic lakes of Poland, as well. In their resting stage, from late June to October, the copepodites of these species live in the bottom sediments which contain sulphuretted hydrogen. The specimens of *C. bohater* and *C. v. vicinus* plunge into the mud at a depth of about 9.5–14.5 cm, with the maximum in the upper 2.5 cm (Wierzbicka, 1967; Wierzbicka and Kędzierski 1964).

Data concerning the hydrochemical conditions of the clay-pit are given in the papers by Wierzbicka (1960) and Wierzbicka and Kędzierski (1964).

Both *Cyclops bohater* and *C. v. kikuchii* have their resting stage in the form of copepodites V, *Cyclops v. vicinus* — in the form of copepodites IV.

Table I. Lipids in copepodites during the resting period (clay-pit in Warsaw)

Species	Stage	Date of mud sampling	Number of days of stay in cooler	Number of specimens	Dry weight of one specimen (μg)	Lipids in one specimen (μg)	Lipids in % of dry weight
Cyclops bohater	V	17.VII.1968	20–44	180	30.0	6.09	20.3
		4.X.1968	8–18	169	23.7	4.46	18.8
		4.X.1968	23–44	302	22.2	3.52	15.9
Cyclops vicinus vicinus	IV	17.VII.1968	20–44	252	7.4	0.73	9.9
		4.X.1968	22–43	351	6.0	0.39	6.6
Cyclops vicinus kikuchii	V	17.VII.1968	0–13	804	10.6	0.67	6.4
		17.VII.1968	20–44	1865	9.5	0.78	8.2
		4.X.1968	8–18	865	9.2	1.19	12.9

The copepodites of Cyclopoida reveal typical features, characteristic of the resting period, i.e. the presence of "mud disks" on the either side of cephalothorax, and the specific state of alimentary canal distinguished by the presence of large concretions in the stomach vacuoles, as well as by the presence of crystals in stomach and in plugs that close up the intestine at the levels I and II of abdominal segments (WIERZBICKA 1966, 1967). Shortly after awaking the Cyclops individuals, these crystals and the plugs are thrown outside. The above features of the alimentary system (crystals, large concretions) prove both the metabolic processes and the accumulation of metabolic products in the body of Cyclops.

METHOD

The mud sampled from the clay-pit was taken to the laboratory and stored in a cooler at a temperature of 4°C, in darkness and immobility. The copepodites were taken for analysis from mid July to mid November (Table I). After the copepodites had been got out of the mud they were awaked in an aerated water environment and placed then in small weighing vessels of aluminium foil. Determinations of lipids were made by means of STERN-SHAPIRO's method (1953), however, with a somewhat other process introduced during the extraction of lipids.

For determinations the specimens were placed in dry ice and additionally dried in vacuum above calcium chloride (Siccum) at a temperature of 4–6°C to obtain a constant mass.

Then, the specimens were homogenized with ethyl alcohol, and after the treatment with ethyl ether (mixture 3 : 1 by volume) first extraction of lipids was performed.

After centrifuging and decanting the supernatant, the sediment was undergone second extraction of lipids and heated to a temperature of about 60–65°C in the presence of new alcohol-ether mixture of the same composition. Afterwards, the sediment was centrifuged and the supernatant decanted. Combined

supernatants, filled up to certain volume, were then pipetted for analysis li-
ke in the STERN-SHAPIRO's method.

For comparison standard methyl salicylate solution was used and served
to determine lipids in samples, in terms of animal lipids. For calculation the
mean equivalent weight of esters of aliphatic acids was taken as 320.

The contents of lipids are presented in percentage of dry weight and on
dry weight of one specimen.

RESULTS

Table I shows that *C. v. vicinus* has the lowest dry weight of one speci-
men, *C. bohater*, the highest one. *C. v. vicinus* is more than 4 times lighter
than *C. bohater* and over 1.5 times lighter than *C. v. kikuchii*. This latter is
almost 3 times lighter than *C. bohater*. Attention should be paid that among
all the considered species the unit mass of the bodies decreases with the pas-
sage of the resting period.

In the late resting period decrease of fat balls number was observed mi-
croscopically in the body cavity of Cyclops, e.g., *C. v. kikuchii* and *C. strenuus*.
However, according to BRAND (1946), this does not mean that the lipids have
already been consumed.

The greatest amounts of lipids (Table I) are characteristic of copepodites
of *C. bohater*, the less — of *C. v. vicinus* and *C. v. kikuchii* (at the beginning of
the resting period — 20.3; 9.9; and 6.4 in % of dry weight, respectively).
These are values lesser than those for the copepodites IV of *Cyclops furcifer*
Claus, a species from the astatic basins — 33.9 in % of dry weight (825 spe-
cimens). These were copepodites prepared already to pass into dormant stage
(WIERZBICKA 1967). It is proper to emphasize that the calorific value of the
copepodites IV of *C. furcifer* (1475 specimens), determined in calorimetric
microbomb (after PHILLIPSON 1964), was also extremely high, and was 5.330 cal
per 1 mg of dry weight (as compared with the calorific value of mature fema-
les of an allied species from the astatic basins — *Cyclops strenuus* Fischer —
calculated to be 4.7643 cal/mg (WIERZBICKA 1967)).

There are only scarce data in the literature concerning the amounts of
lipids in Cyclopoida. FARKAS (1958) gives information on a considerable
amount of lipids among the specimens of *Cyclops* sp. from plankton: 40.39;
40.84 and 44.93 in % of body dry mass. However, the species of this Cyclops
is unknown. According to the data presented by BLAŽKA (1966), the specimens
of *Cyclops v. vicinus* (mature individuals+copepodits from plankton) have less
than 6.4% lipids in relation to dry weight. The data obtained by the present
authors for the copepodites *C. v. vicinus* in the resting stage (9.9 and 6.6) pro-
ve, as compared with the results cited by BLAŽKA, the presence of a conside-
rable amount of lipids in the earlier resting development stage (IV).

The analysis of the results presented in Table I demonstrates a double
increase in the amounts of lipids in the late resting period of *C. v. kikuchii*
(from 6.4 to 12.9) and a slight decrease among those of *C. bohater* and *C. v.
vicinus*. The regression curve (elaborated according to an equation $y = a + bx$)
presents that for the examined species of the genus Cyclops, which are in the
resting stage, a general decrease in the amounts of lipids in one specimen takes
place together with the decrease in dry weight of the specimen, with the pas-
sage of resting period (Fig. 1).

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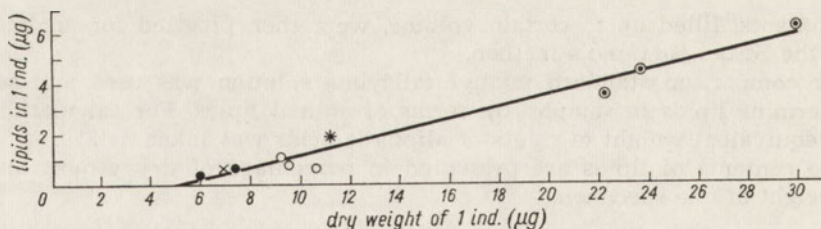
Fig. 1. The regression curve ($y = a + bx$) of the examined Cyclops species in the resting stage

○ *C. bohater* ⎫
● *C. v. vicinus* ⎬mud
○ *C. v. kikuchii* ⎭

× *C. v. vicinus* ⎫
* *C. v. kikuchii* ⎬plankton

At present, the results can hardly be interpreted. It appears that in the case of *C. v. kikuchii*, represented in this examination by most specimens, the picture is highly interesting. Maybe, this picture proves the observations of Blażka that the total amounts of body lipids increase in the case of anoxia (observations on *Carassius carassius* L. Blażka and Kopecky 1963). The differences ascertained to appear in the amounts of lipids may, during the resting period, depend upon the physiologic differences of the examined species, or this may have been affected by the difference in the number of days during which the dormant copepodites were stored in cooler, as well as by the artificial conditions produced during this situation.

Supplement

A comparison was made of the contents of lipids in the copepodites that were in the resting stage, and in those of the same species and of the same state, but active, which lived in the plankton of the clay-pit examined.

The copepodites IV of *C. vicinus vicinus* were sampled from plankton on Feb. 17 and 25, and Mar. 10, 1969, in an amount of 1337 specimens (Table II). 214 specimens of the copepodites V of *C. vicinus kikuchii* were isolated during the same days. Thus, in the planktonic life of these species, this was a period considerably distant from the time when the copepodites plunged into the mud to pass into their resting stage in June.

Table II. Lipids in active copepodites from plankton of a clay-pit in Warsaw

Species	Stage	Date of plankton sampling	Date of isolation of specimens from plankton	Number of specimens	Dry weight of one specimen (μg)	Lipids in one specimen (μg)	Lipids in % of dry weight
Cyclops vicinus vicinus	IV	17.II.1969 25.II.1969 10.III.1969	17–24.II.1969 26–28.II and 13.III.1969 10–15.III.1969	1337	7.0	0.70	10.0
Cyclops vicinus kikuchii	V	17.II.1969 25.II.1969 10.III.1969	17–24.II.1969 26–28.II and 13.III.1969 10–15.III.1969	214	11.2	1.90	16.9

The amounts of lipids in the active copepodites IV of *C. v. vicinus* were slightly higher than in those which were in the resting stage. On the other hand, the active copepodites V of *C. v. kikuchii* were characterized by greater amounts of lipids, as compared with those in the resting stage.

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BIOENERGETICS OF OSMOREGULATION IN AQUATIC ANIMALS

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ABSTRACT

Osmoregulation consists in ion exchange between the organism and environment
as well as the maintenance of differences of osmotic concentration between the
body fluids and the external environment. This requires the expenditure of some
amount of energy. A method for the calculation of this expenditure after Potts
(1954) is given. Drastic changes of the metabolism level (respiration) that ac-
company the changes of the environment salinity are caused by the process of
cellular and tissue adaptation. The animals belonging to populations already adapted
to different salinities have the same level of general metabolism. Examples il-
lustrating the above mentioned phenomenon are given as well as directions in order
to avoid the errors in metabolism estimation under the conditions of changed
salinity.

The osmoregulation of aquatic animals consists in keeping the difference
between the osmotic concentration of body fluids and that of external envi-
ronment, as well as in homoecstatic ion and water exchange between the
organism and environment. The ability to have such a regulation is characte-
ristic of the euryhaline and fresh-water animals, which due to this feature
are called osmoregulators. Type marine animals are referred to adjustators,
or osmoconformers, since they do not regulate their osmotic pressure and are
in an isoosmose state with their environment.

Evidently, the necessity of keeping such a difference by the osmoregula-
tors against the pressure gradient involves in the organisms an energy con-
sumption. It has previously been supposed that the energy consumed must be
considerably high, since any change in the concentration of the environment
caused, as a rule, a high increase in the metabolism of an animal.

The first calculation of such consumption was made by Potts (1954), who
examined three species (*Eriocheir sinensis*, *Potamobius fluviatilis* and *Ano-
donta cygnea*), the parameters of which were known, according to the follo-
wing formula:

$$W = R \cdot T \cdot U \cdot V \cdot \ln \frac{B}{M} \text{ cal/hr,}$$

where:
W = osmotic work, cal/hr,

R = universal gas constant = 1.986 cal/hr,
T = absolute temperature,
V = volume of the urine produced, l/hr,
U = urine concentration, mol/hr,
B = blood concentration, mol/hr,
M = environment concentration, mol/hr.

The analysis showed that, contrary to all expectations, the thermodynamical costs of osmoregulation are, on the average, more than 1% of the total metabolism. In the case of Potamobius $W = 0.0367$ cal, of Eriocheir — 0.0757 cal, and of Anodonta — 0.0105 cal, on 60 g of the body weight per 1 hr, this being respectively 0.3, 0.5 and 1.2% of the total metabolism.

The direction of physiological adaptation of marine animals that, during their evolution, enter brackish or fresh waters, secures the lowest costs as possible. This aim is usually obtained either by a direct decrease in blood concentration, or (in the case of fresh-water animals) by the production of hypotonic urine. Potts presents his calculations of the considerable savings in energy obtained in this way. For example, *Eriocheir sinensis*, that drops its blood concentration from 1.2 to 0.32 mols per 1 litre, may decrease twenty times its output for osmoregulation. As concerns Potamobius, this problem is as follows: low blood concentration (0.42 mol/l) and production of hypotonic urine (0.124 mol/l) decreases this output 35.4 times. Anodonta, which is a form characterized by the lowest blood concentration among all the known animals, decreases its output for the osmoregulation several thousands times.

Most probably, the actual losses are somewhat higher, since in his theoretical model Potts assumed the ideal semi-permeability of the organisms analysed, and did not consider the losses in ions on the body surface; and therefore was criticized by Croghan (1961).

Ions lost by organisms in a hypotonic environment are recovered from food, by the active transport through gills from the environment, and by the resorption that takes place in the excretory organs. Since this is a process that proceeds at the cellular level, its thermodynamical costs cannot be determined at present in detail. Having this in view, Potts (1954) applied an equation for a reversible process. For a two-ion solution (e.g NaCl) the equation looks as follows:

$$\Delta G = 2R \cdot T \cdot \ln \frac{cA}{cB},$$

where: G determines the amounts of the energy necessary to carry 1 mol of a solute from concentration cA to concentration cB. Croghan (1961) is of the opinion that this equation is satisfied only when the relation cB/cA is in an equilibrium throughout the whole process. In fact, the active transport is here an irreversible process and expresses the disturbance in equilibrium. During the ion transport their free energy is smaller than that obtained from the hydrolysis of the high-energy phosphoris bonds. A considerable portion of the energy obtained from hydrolysis is emitted in the form of heat.

The same author emphasizes also the structure of the excretory organ formed as an elongated tube, interesting from the viewpoint of osmoregulation economy. Such a structure enables the formation of the zones characte-

rized by various gradient of concentration, between the excretion fluid and the epithelium of tube and blood, being probably favourable for saving the energy during the active resorption of ions.

Phenomena which are the result of Donnan equilibrium are also sources of this economy. When ions are lost, part of pressure that is wanted to the state of osmotic equilibrium may be covered by organic non-electrolytes liberated or kept in blood. As a rule, this role is played by free amino acids or urea. On the other hand, proteins found to occur in the fluids of body may bind ions into non-diffusive complexes that, among others, reduce in this way the loss of ions to a hypotonic environment (POTTS and PARRY 1964).

Apart from the reservations and complements presented above, the model suggested by POTTS seems to be the only one that allows us to estimate quantitatively the thermodynamics of part of metabolism related to osmoregulation. If, however, the losses in energy are here insignificant, a question arises how to explain the changes (up to some dozen per cent) that appear in the metabolic process of animals after the variations in salt contents of the environment (Fig. 1).

This phenomenon may be elucidated by processes at cellular and molecular levels. The change in environment salinity is responsible for a change in water contents in the tissues, for a change in the gradient of certain ions (mainly K^+ and Na^+), for the oxygenation of amino acids in blood, or inversely, for the
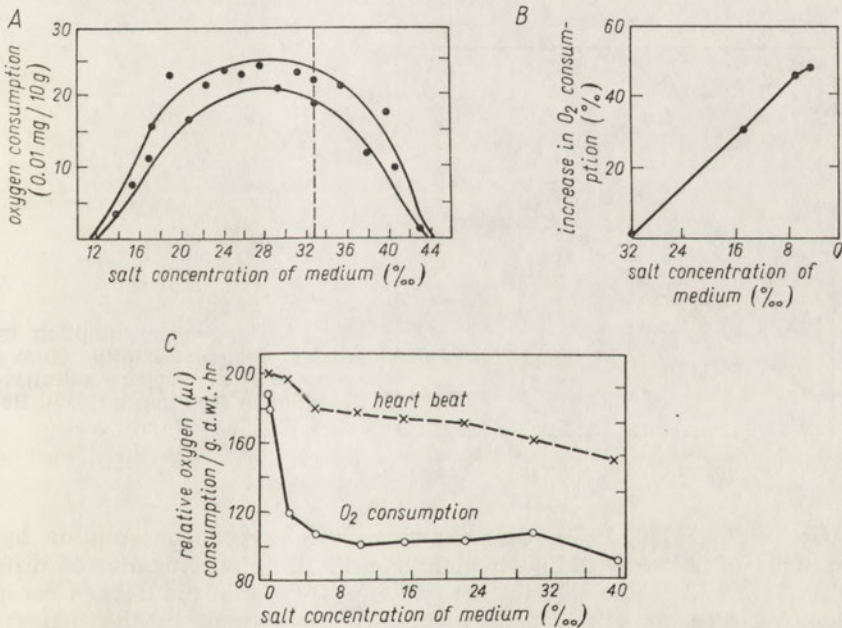
Fig. 1. Changes in metabolism of euryhaline animals, caused by a change in the salinity of environment. A — effect of salinity upon oxygen consumption by *Mytilus edulis* var. *galloprovincialis*, in 12.5°C. Dotted line shows the salinity of normal biotope. According to BOUXIN (1931); B — effect of salinity upon oxygen consumption by *Carcinus maenas*. According to SCHWABE (1933); C — effect of salinity upon oxygen consumption and frequency of heart beat in *Gammarus duebeni*; males, temp. 20°C. According to KINNE (1952)

liberation of bounded amino acids, and for the swelling of mitochondrions. All these processes, which are here a result of the disturbed homoeostasis of the organism, lead to a periodical increase in tissue and general metabolism (Fig. 2), up to the new steady state, when the metabolism returns to the previous level (according to KARANDEEVA 1966). In consequence of
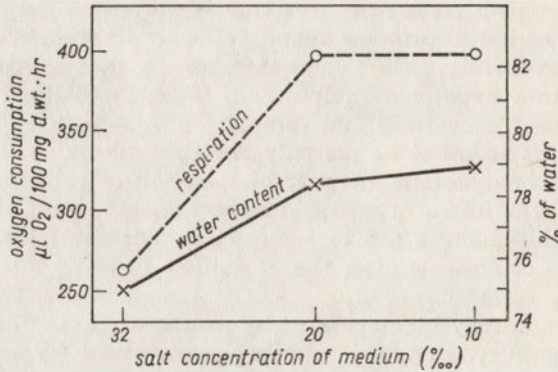
Fig. 2. Respiration and water contents in gill tissue of *Carcinus maenas*, depending on the environment salinity. According to PIEH (1936)
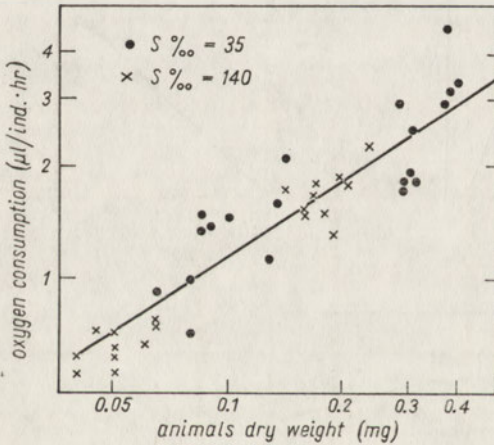
Fig. 3. Oxygen consumption by females of *Artemia salina* from environments of various salinity. According to GILCHRIST (1958). Both in logarithmic scale

this, GILCHRIST (1956, 1958), who examined the oxygen consumption by two populations of *Artemia salina*, which live in the environments of different salinity (35‰ and 140‰), did not note any differences in the oxygen consumed by females (Fig. 3). Differences that were ascertained in the males were caused by a dissimilarity in their morphology in both populations.

As a rule, after a longer adaptation of animals to the conditions of new salinity, their metabolism comes back to normal (BEADLE 1931, RAO 1958, RAO and MADANMOHANRAO 1963). Changes in the intensity of respiration depend in this case upon the rate of the change in the salinity and upon its amplitude (KARPEVIC 1947, 1955, 1958). The more rapid is the change, the greater is

its effect on metabolism. In the case of gradual, slow adaptation, the respiration may practically be unchanged. Numerous works by SOLDATOVA and TURPAYEVA on this subject are exhaustively discussed by KARANDEEVA (1966).

Of similar nature is here the problem of output for osmoregulation in fresh-water animals, adapted to brackish water, as well as in organisms of fresh-water origin, adapted to hyperhaline waters (salines). Here, the direction of osmotic stress changes, and the animals must protect themselves against the excessive penetration of ions into the inner medium. Among the halophilous organisms the relatively constant blood concentration is maintained due to a low permeability of body cover, active removing of ions from kidneys and water absorption in the intestine. Moreover, they also use their compensation mechanism known as "Donnan principle".

In the case of adaptation of fresh-water animals to brackish environment, their metabolism remains unchanged. This may be illustrated by the author's results. Imagine an animal in such a stage of its ontogenesis, in which it does not assimilate food, derives its energy merely from the reserves accumulated in its body, and lives only until the reserves are exhausted. In this case the similarity of life span of the populations acclimatized to the environments, characterized by various salinity, will prove the similar energy costs of maintenance in these environments. Animals of such a type, i.e. miracidiums of *Fasciola hepatica*, have been adapted to the medium of diluted sea water, from 1 to 13‰. It appeared that the larvae adapted during the embriogenesis to the environment of various salinity have, after hatching, the same life spans as the control population from fresh water, and show the same activity, proving the identical energy consumption (Fig. 4).
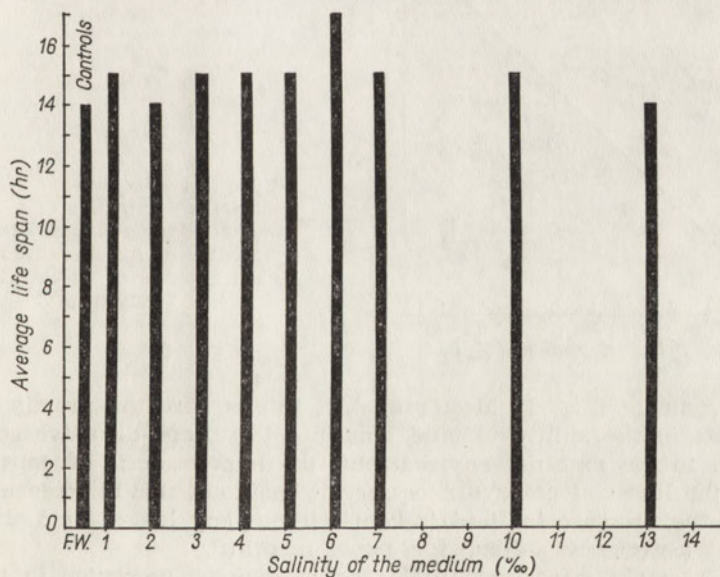
Fig. 4. Mean life span as an index of intensity of metabolism in miracidia of *Fasciola hepatica*, adapted to the medium of various salinity. According to STY-CZYŃSKA-JUREWICZ (1965)

The relations observed to exist in the eggs of the fresh-water snails are an example of the role played by organic molecules, which consists in a decrease in losses of energy that is necessary to keep a constant difference of concentrations between the inner and outer environments. Egg and then embryo are closed in a hyaline capsule that contains rich nutrient substances in the form of colloidal solution of proteins and galactogen. This fluid is characterized by an autonomic ability to keep the hyperosmosis in relation to the
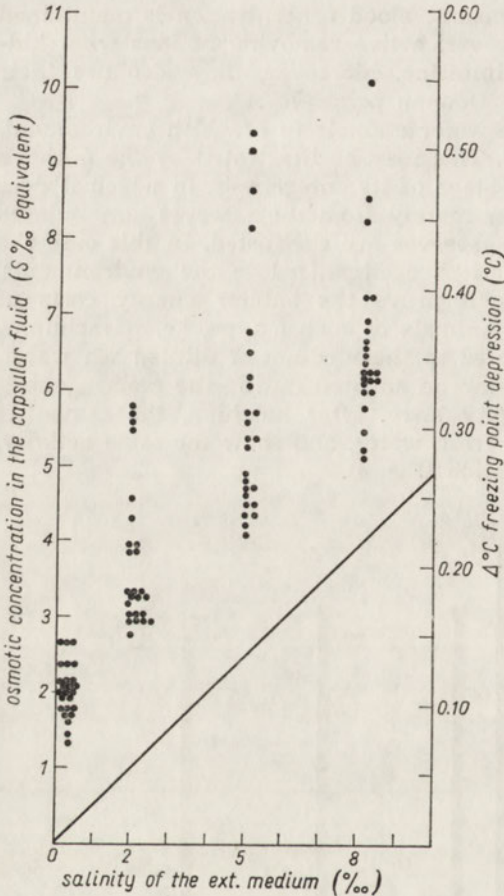
Fig. 5. Hyperosmosis of capsular fluid in egg capsules of a fresh-water snail *Physa acuta* Drap., in an environment of increased salinity. Measurements of $\Delta°C$ after 20 hr stay at 5°C

outer environment (Fig. 5). Most probably, this is here the protein property that consists in the ability to bind ions into loose, non-diffusive complexes. In relation to the external environment, the hyperosmosis of capsule fluid decreases the losses of embryo necessary to maintain this difference in pressures, and the pressure in fluid is kept without any losses for active transport of ions (STYCZYŃSKA-JUREWICZ, paper in print).

All the remarks mentioned in this paper may be presented in the following points:

1. Thermodynamical costs for osmoregulation are low. These may be only slightly greater than 1% of the total metabolism.

2. An organism may decrease these costs by lowering both blood and urine concentrations. Energy losses arisen as a result of an active transport of ions are reduced, due to the decrease in the permeability of body cover, to a development of the apparatus cf inner resorption of ions, as well as to Donnan effect.

3. Changes in metabolism, observed to appear during the variation in salinity, are caused by the process of physiological adaptation, and disappear after the termination of this process.

4. This phenomenon should be taken into account during the research on the metabolism in different salinity, when adequately long-lasting adaptation under the conditions that accelerate the metabolism of animals is necessary.

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FOOD RATION AND THE TIME OF REDUPLICATION OF *DILEPTUS CYGNUS* CLAP. ET LACH. POPULATION IN DIFFERENT FOOD CONDITIONS

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ABSTRACT

Doubling consumption rate, generation time and population mobility of a predatory ciliate, *Dileptus cygnus* were investigated. Conditions in which there were 5 preys (*Colpidium colpoda*) per predator, were the most favourable for population growth of Dileptus. When the food supply was below or above optimum, generation time became longer, the value of doubling consumption rate and population mobility were higher.

The results, which shall be presented are a part of investigations on elements of energy balance of a predatory infusorian *Dileptus cygnus* Clap. et Lach. Very few papers deal with the bioenergetics of prctozoans. Salt (1964, 1967, 1968), when investigating the feeding of Woodrufia and *Amoeba proteus* provided some data on the food ration of these protozoans understood as a number of prey eaten by the predator in between the successive fissions. However, the factors, which affect the consumption, biomass increase and other elements of energy balance are not well known yet. It can be expected that one of such factors are the food conditions.

This paper deals with the effect of food conditions on the development of experimental populations of predatory infusorian *Dileptus cygnus* with special attention to the increase in number, food ration and the time of population reduplication.

METHODS

The protozoans were cultivated in Petri dishes, in 20 ml of Prinqsheim solution and at a temperature 22°C (± 2°C). The animals were fed every day with different infusorians, *Colpidium colpoda*, in such a way that a determined number of potential prey, i.e. Colpidium fell per each Dileptus. Four variants of the food indicator were applied $\left(\dfrac{\text{density of Colpidium}}{\text{density of Dileptus}} = \dfrac{D_c}{D_D} \right)$:

1, 3, 5, and 10 including the range from food defficiency to its surplus (acc. to the estimations from previous investigations).

Two conceptions of the food ration were used: 1) daily consumption rate, i.e. average number of preys consumed by one predator within twenty four hours, 2) doubling consumption rate, i.e. average number of preys consumed by the predator from the beginning of exposition to the moment in which the population number is reduplicated.

Daily consumption rate was determined from the difference between experimental samples (with the predator) and control ones (without the predator) applying the Gauld's formula:

$$R = \frac{C_k - C_t}{t} \cdot \frac{2C_0}{C_k + C_0} \cdot V$$

where:

C_0 — initial density of prey,
C_k — density of prey in control after t time,
C_t — density of prey in an experimental test after t time,
V — volume of the sample.

Doubling consumption rate was calculated out of the daily consumption rate and the time of population reduplication, i.e. time after which the population number is doubled (acc. to SALT 1968).

The population number was estimated out of the every day markings of the density of Dileptus in the culture.

RESULTS

The rate of increase of the population number of *D. cygnus* depends on the food conditions of the population (Fig. 1). Populations in which 5 potential preys fall on one predator have the most dynamic development. In conditions where the value of food index is lower or higher than 5, the increase rate of the population number is weaker.

Differences in the dynamics of population development seem to be closely connected with the effect of food conditions on the food ration and time of population reduplication. Together with an increase of food index daily consumption rate increases adequately, while at the same time this increase is slight when the value of food index is more than 5 (out of 10 potential preys 5-7 are consumed during 24 hours) (Fig. 2). But the doubling consumption rate decreases at an increase of food index achieving the minimum at $\frac{D_c}{D_D} = 5$.

At a further increase of $\frac{D_c}{D_D}$ the doubling consumption rate increases again. The character of its changes is convergent with the changes of generation time in the investigated range of food conditions. Together with an increase of daily consumption rate the time of reduplication of the population number is shortened. It is again the shortest in conditions where 5 preys fall on one predator. When there are more preys in the medium $\left(\frac{D_c}{D_D} = 10\right)$ the time of population reduplication increases again. This is why the value of doubling consumption rate is so high at a small increase of the daily consumption rate.
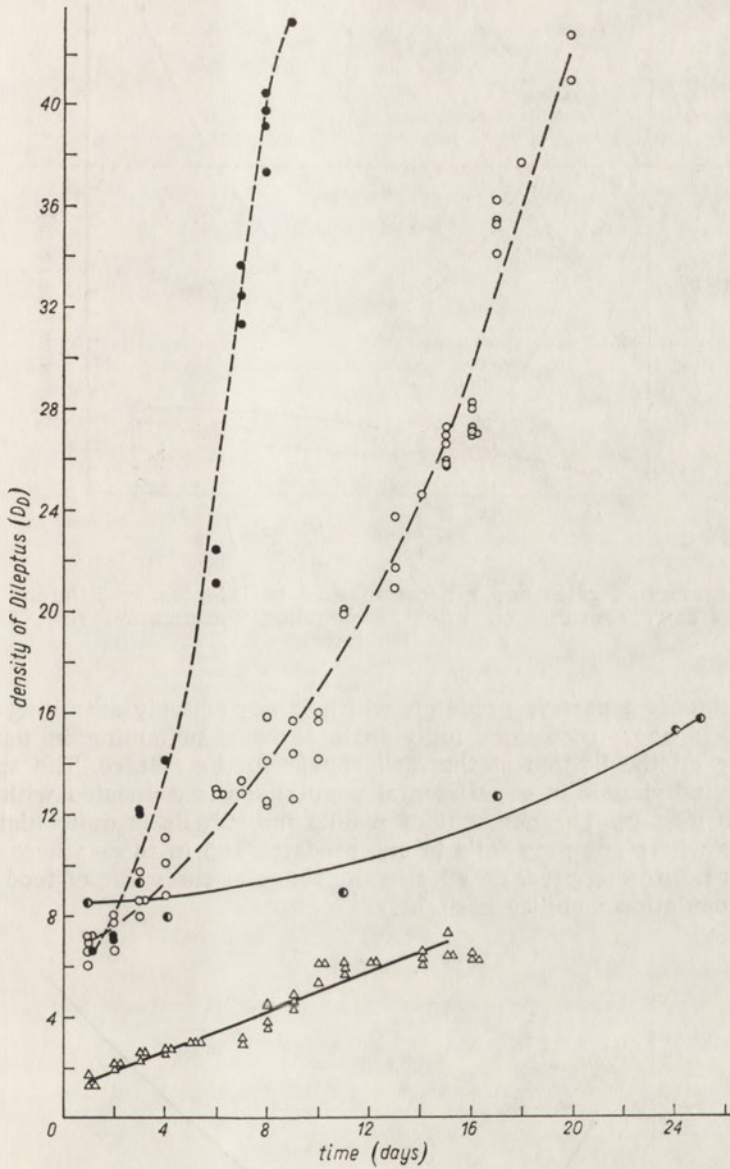
Fig. 1. Development of *Dileptus cygnus* populations in different food conditions. ◗ — development of Dileptus population at $\frac{Dc}{D_D} = 1$, ◯ — at $\frac{Dc}{D_D} = 3$, ● — at $\frac{Dc}{D_D} = 5$, △ — at $\frac{Dc}{D_D} = 10$
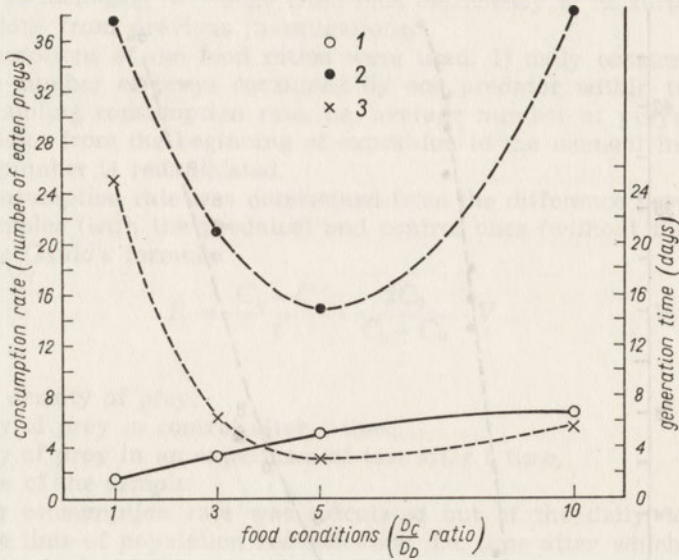
Fig. 2. Consumption rates and generation time of Dileptus in different food conditions. 1 — daily consumption rate, 2 — doubling consumption rate, 3 — generation time

D. cygnus is a passive predator, which is not actively searching for prey. However, in some conditions individuals actively swimming in the solution or moving on the bottom of the dish appear in the culture. The appearance of mobile individuals in experimental populations is connected with the food conditions (Fig. 3). The per cent of mobile individuals is quite high both in conditions where one prey falls to one predator and in those where 10 potential preys fall to one predator. But in the range of the value of food indicator 3–5 the population mobility is slight.
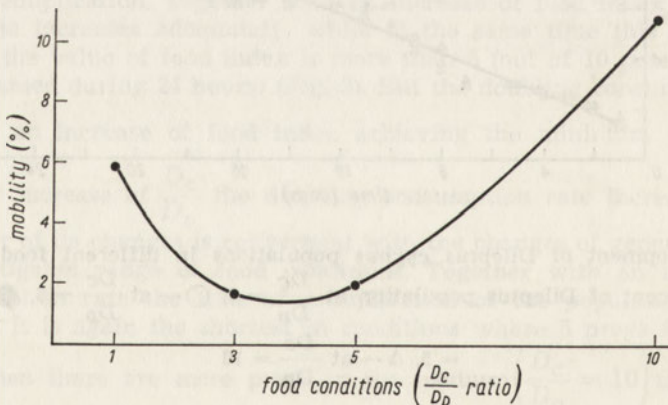
Fig. 3. Mobility of Dileptus populations in different food conditions

DISCUSSION

The described investigations were carried out in order to find whether the investigated range of food conditions covers also such which could be defined as the most favourable for the development of *D. cygnus* population. It might have been assumed that in the food optimum the time of population reduplication should have the lowest values.

The fact that the population development is the most dynamic at a food index equals 5 (Fig. 1) would suggest that these are the best food conditions. Also in these conditions the generation time is the shortest, which conditions its quick increase. Similarly the doubling consumption rate is the lowest in these food conditions (Fig. 2). These data are a sufficient proof that conditions in which there are 5 preys per one predator are really the best conditions. Taking into consideration the time of population reduplication, doubling consumption rate and the rate of biomass increase, the conditions determined by food index equal 1 should be considered as conditions of food deficiency, and those, where the food index is 10 as conditions of considerable food surplus. In both these extreme cases the time of population reduplication and the doubling consumption rate have much higher values than in the food optimum.

Both in conditions of defficiency and surplus of food in the medium the per cent of mobile individuals in the population increases but is small in the food optimum (Fig. 3). The reasons for an increasing mobility are most certainly different in case of food defficiency and surplus. In the former case the appearance of mobile individuals is caused by hunger (very small daily consumption rate). In the latter case the increased mobility of Dileptus might have been caused by worsening medium conditions as a result of accumulation of metabolism products of numerous Colpidium, half of which is hardly consumed during twenty four hours. This also probably explains why the time of Dileptus population reduplication is longer in these conditions.

It seems that only in conditions when the predator has at disposal such a number of prey, which can be consumed quick enough as to avoid too great accumulation of the products of their metabolism, predator population can develop without disturbances caused by food defficiency or surplus and connected with the latter noxious effect of metabolites. These conditions are fulfilled when the food index $\frac{D_c}{D_D} = 5$. In this case the mobility of predator population is small as there is a sufficient number of prey for the predator, and the accumulation of metabolites does not cause yet an increase of this activity.

This confirms the previous conclusion namely that at $\frac{D_c}{D_D} = 5$ the food conditions were the best for the development of investigated *D. cygnus* population.

Undoubtedly this food optimum may be moved in the direction of higher and lower $\frac{D_c}{D_D}$ index depending on, e.g., temperatures, density of predator population and so on. This is the subject of further investigations.

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HYDROBIOLOGICAL AND BIOENERGETICAL INVESTIGATIONS IN THE NENCKI INSTITUTE OF EXPERIMENTAL BIOLOGY

(A HISTORICAL SURVEY)

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I. THE PERIOD BETWEEN WORLD WARS

The progress in Polish hydrobiology during twenty years between the world wars was connected to a greater extent with the fate of the M. Nencki Institute. As early as in the first years following the Institute foundation, its Presiding Board has agreed over a primary goal to form an experimental station devoted to investigations of freshwater biology. The hydrobiological Station at Wigry, founded in 1920, located in a provisional building at first and later transferred to a new building, had a priority in using for many years the financial means of the Institute. To give an example, in the years 1925–1930, the Station at Wigry has spent about one third of the total budget of the Institute for its constructional equipment, and other needs.

Another evidence of the care and attention paid by the Nencki Institute to the hydrobiological investigations was foundation of the Marine Station at Hel in 1932. This enabled on both the freshwater and marine investigations to be represented among the Institute activities. A further development and extension of hydrobiological research were preliminary studies of the rivers carried cut in the region of Polesie since 1929. This activity led to foundation of the Biological Station in this region (1937), the main aim of the station being the studies of rivers and marshes.

With the above mentioned centres, the following names of their organisers and heads are connected: A. Lityński, M. Bogucki, and J. Wiszniewski, the prominent scientists of the Polish hydrobiology and co-founders of the world limnology and oceanology.

The station at Wigry had an excellent opportunity for limnological investigations due to its location over a relatively young, deep, and little entrophized, lowland lake. In a close vicinity of Wigry, within the reach of the Station transport facilities, there are over 20 water bodies of a very differentiated character, mostly of oligotrophic or distrophic character.

The marine Station at Hel has initiated oceanological research in Poland; many of scientists of an older and middle age generations at present being trained and educated in its laboratories. The rapid progress of the Biological Station at Polesie despite of its narrow activity, points to its good lacation and organization.

This review of the pre-war activity in the Polish hydrobiology will hold only a few examples of research carried out in the hydrobiological centres of the Institute. One should bear in mind that the permanent staff of these centers was small as compared with the number of guests who worked temporarily or seasonally at the Stations of Wigry, Hel, or Polesie. One cannot overemphasize the fact that almost each of Polish hydrobiologists active at that time has spent some time in one of the above mention centres of the Nencki Institute.

Apart from supplying the facilities for hydrobiological investigations, these centres were field bases for all kind of faunistic and floristic explorations, as well as for experimental work with easily available fresh live material derived from natural environments. Papers by Wiszniewski on psammon rotifers unite high taxonomo-morphological standard with ecological merits, Z. Koźmiński, dealing with morphology and taxonomy of copepods belonging to the "Cyclops strenuus" group left a precious study of application of biometrics and statistics to the problems of zoological taxonomy. Equally valuable are his papers on distribution of chlorophyll in lakes of different types. Papers by Geysztor dealing with small ponds are classical amongst studies of astatic waters. Numerous papers by A. Lityński comprising treatises and theoretic considerations of communities of aquatic environments are especially interesting. J. Wołoszyńska has started her algological research in the Field Station at Wigry and K. Demel — his studies on hydrography and biology of the Baltic Sea at the Marine Station at Hel. Demel's studies on the bottom fauna can be considered as a basis for further syntheses pertaining to the dynamics of benthic community biomass. Papers on osmoregulation in fish roe and echinoderm eggs, and in hemolymph of crustaceans, carried out by M. Bogucki, belonging to the classics of the world literature concerning this problem. Papers by M. Stangenberg on chemistry of lake waters and on typology of lakes of this region were written at the Wigry Station. I. Cabejszek continued algological studies of the Polesie region, and F. Krasnodębski — morphology, taxonomy, and biology of Cladocera. Experimental work by K. Passowicz on adaptation of Cladocera to environmental conditions deserves a special attention as new and creatine at his period of hydrobiological research, this approach having so many followers later.

The outline of hydrobiological centres of the Institute during the period between the world wars would not be complete one without mentioning their teaching activities during the summer courses held at the Station of Wigry and at the Marine Station, as well as the publishing of "Archiwum Hydrobiologii i Rybactwa", one of the first hydrobiological periodicals issued all over the world.

II. THE POST WAR PERIOD

After the war, the Nencki Institute started a new its usual research work, in the field of hydrobiology in spite of a very severe loss both of its staff and equipment which suffered the Polish hydrobiology. Z. Koźmiński and J. Wiszniewski were killed during the war, A. Lityński was lost in the chaos of the final war period, and many hydrobiologists were scattered throughout the world.

HYDROBIOLOGICAL STATION AT MIKOŁAJKI

The restitution of the Wigry Station did not seem appropriate since the new frontiers of Poland included a vast region of lakeland and the group of Wigry lakes became situated on the periphery of this area. In 1951, the Nencki Institute made further progress in the hydrobiological research by organizing the Hydrobiological Station at Mikołajki, in the Masurian Lake District. The Station was led by A. SZCZEPAŃSKI.

This Station was owned by the Institute until the end of 1961. Following the tradition of the Wigry Station, this centre was meant to form an ample basis for work of other biologists from the Institute Departments as well as from outside of it besides the original investigations carried out by its permanent staff. In that period the original investigations aimed at recognition and exploration and cataloguing the lakes and other water bodies of the Masurian Lake District, situated in the proximity of the Station. The work of A. SZCZEPAŃSKI comprised mostly physical and chemical conditions of these reservoirs, specially optical properties of lake waters and the comparative, hydrological and hydrochemical characteristics of lakes of the basin of River Krutynia.

W. SZCZEPAŃSKA studied Trichoptera of the Masurian Lakes and the dynamics of water masses in relation to the configuration of the shore line, Z. MALANOWSKI dealt with phytoplankton, S. KOSICKI studied communities of rotifers, and A. KOSICKA — the biology of reeds.

The Station at Mikołajki, similar as its predecessor at Wigry attracted hydrobiologists of various centres; it organised courses for young scientists and the students practicals.

THE DEPARTMENT OF EXPERIMENTAL HYDROBIOLOGY

The organising of the Department of Experimental Hydrobiology within the Nencki Institute in Warsaw at the end of 1953 was a further step in the hydrobiological studies done by the Nencki Institute.

During the first ten years of the Department existence the research was mainly focused around the problems of biology of astatic water bodies, especially on periodically vanishing ponds. There were numerous reasons which decided upon this line of research.

Small ponds were but little investigated hydrobiologically at that time, their economic significance and validity for various studies being generally neglected. The most of the Polish territory is almost void of lakes, being thus an area of the increasing water deficiency, which can be seen, among other symptoms, from the steppe succession occuring in this terrain. In this area, small ponds together with fish ponds decide to a greater extent upon the retention of water, water balance of the atmosphere, and thus upon the local climate. The astatic property of this environment has a special value from the scientific point of view. It facilitates examination of the effect of varying conditions of the habitat (e.g. drying, freezing, salinity, daily and seasonal changes in temperature, oxygen concentration, etc.) on the organisms which live in an astatic environment. Such phenomena as anabiosis, competition for food, population structure, interdependences between the links of biological production, etc., become especially sharply outlined these reservoirs, this helps to study these phenomena in the field or in the laboratory experiments.

The majority of the field work has been carried out on the small ponds of

the Eastern part of the Kampinos Forest, situated on a dune-marsh terrain of the Vistula pre-valley, north-west of Warsaw. The extensive field studies, either directly concerned with this problem (CHODCROWSKI and CHODOROWSKA 1958, PASCHALSKI 1959a, CHODOROWSKI 1961a), or related to other studies, allowed to outline the regional typology the astatic of small ponds in this area, with distinguishing ephemeral (lasting up to 2.5 months), spring to summer (up to 5 months), and permanent ponds. Investigations of the abiotic environment, mainly of temperature and the chemical properties of water (PASCHALSKI 1958, CHODCROWSKI 1961b, E. FISCHER 1960, 1961, STYCZYŃSKA-JUREWICZ 1962a) gathered a vast material to illustrate the range of variation of these factors in different types of astatic waters within daily and seasonal cycles. Similarly at the changing temperature of an astatic pond within 24 hr can imitate an annual cycle the changes in trophic conditions of such pond can imitate many years' changes in the lake, ranging from the spring oligotrophy to summer or autumnal eu- or distrophy (PASCHALSKI 1958). Daily variation in oxygen content (5–120% of saturation, STYCZYŃSKA-JUREWICZ 1962a) ca reflect the degree of the astatic condition of small ponds. It can be supposed that for living organisms it is more important the intensity of eu- or aperiodism, in other words, daily and seasonal regularity of these changes than the actual range of the environmental conditions (KLEKOWSKI 1966).

Comparative studies of the abiotic environment were sometimes carried out on more eustatic ponds located in another area. Many of these works have been performed with cooperation of the Hydrobiological Station at Mikołajki.

Papers by PASCHALSKI (1959d, 1960a, 1960b, 1961, 1962, 1963a, b) much comprise new and interesting information on the thermal, chemical and dynamic properties of lake waters and of various types of mountain reservoirs, on their buffering abilities, describing their general limnetic character. CHODOROWSKA and CHODOROWSKI devoted a number of papers (1959a, b, 1961) to highly eustatic and aperiodic environments; such as cave waters. KAMLER (1965, 1966) dealt with astatic conditions of temperature in mountain waters, showing that in these environments considered usually as stenothermic, the variation in water temperature shows a considerable differentiation and daily rhytms connected with the character of the reservoir. The faunistic and autecological approach was especially developed in the first years of the Department activity. These studies comprised mainly the astatic waters, supplemented from time to time by the data on other types of reservoirs, in order to be able to draw comparative findings. CHODOROWSKA (1961) has described the fauna of nematodes (Nematoda) of 56 small ponds of the Kampinos Forest, where she related the occurrence of these animals to the limnological type of the environment. CHODOROWSKI published a number of papers dealing with flatworms (Turbellaria) (1959, 1960a, b, c, 1961c), describing their occurrence, distribution and biology, especially with in the communities which inhabited the lake littoral. He has distinguished so-called taxocenes or communities of species which belong to higher taxcnomic groups co-occurring in a given biotope and revealing certain dominance structure.

Z. FISCHER in her earlier studies dealt with larvae of dragonflies (Odonata) (1959, 1961a, b). The comparison of dragonfly communities occurring in astatic ponds of morene landscape around Mikołajki and in the Kampinos Forest did not show any difference in the dynamics of seasonal changes in the occur-

rence of these animals, but the species composition was found to depend on the duration of the ponds. A more detailed analysis was devoted to the genus of Lestes, which is typical for vanishing, shortlasting reservoirs (Z. FISCHER 1964a). It was found that the larvae showed some preference to certain aquatic plant communities. This preference resulted from so-called structural pattern of the vegetation of rathan than from its species composition.

KAMLER (1964, 1965, 1966, 1967) has dealt with autecology of the Plecoptera and Ephemercptera larvae of mountain streams, studying the effect of water movement, temperature conditions and astatic properties of the habitat on the quantitative and qualitative occurrence of these insects.

WIERZBICKA, after having dealt mainly with morphology and taxonomy of Copepoda (1959a, b, 1960) became interested in the resting stages of these crustaceans (WIERZBICKA and KĘDZIERSKI 1964, WIERZBICKA 1962, 1966). The resting stage appears to be a very common stage in Copepoda, Cyclopoida; it occurs in all species of this group inhabiting the astatic ponds and lake environments. STYCZYŃSKA-JUREWICZ dealing with biology of parasites studied mainly the larvae of Trematoda of astatic environments. A monography on taxoncmy of *Plagiorchis elegans* (1962b) including its life cycle, with occurs mostly small ponds can be an example of such studies.

Papers by WYSOCKA-BUJALSKA (1958b, 1961) were aiming at determination of annual dynamics of periphyton biocenoses in astatic ponds and running waters; in the latter case, the periphyton was also used as an indication of the water purity. Other papers by this author pertained to the role of substrate for development and growth of diatoms (1959a), as well as to the biology of algae (1959b, c, 1963).

E. FISCHER studied dynamics of bacterial flora of small ponds in extremely different biotopes. In eustatic cave waters (1959), the bacterial flora, reach in species, showed very low activity. In astatic ponds of the Kampinos Forest (1961), on the other hand, the activity of bacteria belonging to different groups, being generally at a very high level, was not proportional to their abundance.

Another group of paper dealt with the specific properties of the animal communities inhabiting astatic ponds (CHODOROWSKI 1958a, b, c, 1961a). In the ephemeral spring ponds (existing up to 2.5 month) the succession of dominant species was found to occur until the complete disappearance of water. Experimental prolongation of the existence of pond brought about a considerable alteration of the community and formation of many-species competition systems typical for permanent ponds. Such succession of dominant species lead probably to a better utilization of reach but monotonous food supply of the ephemeral pond. The conditions found in astatic ponds have also some influence on the specific parasite-host relationship (STYCZYŃSKA-JUREWICZ 1958, 1959, 1962a, 1966), which can be characterized by high intensiveness and extensiveness of parasite invasion, with a relative scarcity of species composition both of parasites and of their hosts.

Another important stage of research of astatic waters consisted chiefly of experimental works, concerning the physiological adaptations of aquatic animals to the astatic conditions of their environments and highly differentiated abiotic and biotic conditions. A description was made of various physiological and ecological adaptations to specific properties of astatic ponds, such as partial or total lack of water for a shorter or longer period during the annual

cycle. The resistance of *Planorbis* sp. (Gastropoda) (KLEKOWSKI 1959, 1961c) to drying factor was higher if before the complete drying of the habitat the snails were kept at a high density. Under natural conditions, such increase of density can be a signal of approaching the drying period and this leads to the increased resistance against the harful factor, which follows the "signal" regularly. When undergoing drying the animals which are adapted to a periodical lack of water (e.g. some Gastropods), loose rapidly come quantity water, mainly in the expense of water present in the hemolymph (KLEKOWSKI 1961a, b, 1963a, b), whereas the remaining water is retained at an almost constant level for a long period, with the intensity of metabolism decreasing considerably as early as at the first rapid decrease of water content. In species poorly adapted to a periodical drying (e.g., some leeches) high loss of water content with a simultaneous increase of metabolism lead to death. During the process of drying, the osmotic pressure in hemolymph of snails increases considerably, and the animals show a certain ability of active osmoregulation to restrain the excessive increase of osmotic pressure (KLEKOWSKI 1963a,b). In the sea water, the osmotic pressure of hemolymph was found to increase reaching a similar level but on account of penetration of ions from the outer environment and not because of dehydration of the organism. The difference in osmoregulation mechanisms in animals exposed to drying or in those treated with sea water is corroborated by the negative effect of sea water on survival of animals during the later period of drying (KLEKOWSKI 1961a, b, c). *Littorina littorea* (Gastropoda), which occurs in a very astatic costal zone shows the smallest resistance to the decrease in salinity when the latter amounts to about 5‰ (KLEKOWSKI 1963a) at higher salinities, the animals are able to survive in the active state, but at lower ones they react by a temporal isolation from the outer environment. When exposed to drying, these animals loose water from the mantel cavity, retaining its storage in the tissues and haemolimph. The ability to compress gases in the pulmonal cavity by a snail *Coretus corneus* is a specific type of physiological adaptation to survive the drying period (KLEKOWSKI 1961a, b, c).

Studies were also made, of concerning the effect of drying and of changes in osmotic pressure of the habitat on the developmental stages of some crustaceans. The eggs of *Triops cancriformis* (Euphyllopoda), considered hitherto as most resistant to drying, showed this property not earlier than after reaching the stage of gastula, i.e., starting from the 6th day after being laid by a female (HEMPEL-ZAWITKOWSKA and KLEKOWSKI 1968). However the humid air saturated with water vapor is a medium in which the development can easily occur, similar to that in water. The increased osmotic pressure, e.g. the diluted sea water stimulates the hatching of Triops eggs, increasing the percentage of hatches (KLEKOWSKI and HEMPEL-ZAWITKOWSKA 1968).

A temporal shortage of water in astatic pond also modifies the rate of development of animals inhabiting it, both in phylogenic sense, which has been known for long and also in ontogenetic one. The mosquito larvae of Aedes genus (CHODOROWSKI 1958c) grow faster when the pond is drying. Similar effect can be reached by an experimental crowding of the population. The changes in volume of the experimental habitat, and in concentration of dissolved metabolic substances (Z. FISCHER 1960) were observed to bring about generally small changes in the rate of development and reproduction of Daphnia (Cladocera) and in the development of Lestes larvae (Odonata), but the

clear negative effect of the increased concentration of metabolites was appearent. An accelerated development of individuals living in periodic waters as compared with those inhabiting permanent ponds, evokes a high food demand, which can be sometimes satisfied by cannibalistic predation. In the case of disappearance of Aedes larvae (Odonata), which in small ponds are a normal food item of larvae of Mochlonyx (Diptera), the latter can complete their development feeding exclusively on individuals of its own species (Chcdcrowski 1958a, b, c, 1961b).

Similar situation was observed in the larvae of Lestes (Odonata), where cannibalism was present even at the excess of food. It did not show any harmfully effect on the development of the surviving individuals, and they were able to complete their development undergoing metamorphosis (Z. Fischer 1961a, b, 1964b).

Styczyńska-Jurewicz became interested in the problem of adaptation of larval stages especially Trematoda to astatic conditions of the environment. Under anaerobic conditions the development of *Fasciola hepatica* eggs (Trematoda) was hindered, all of the eggs being viable for 2.5 months at 28°C. Long-term drying of snails infected with fluke was found to decrease their survival. However the larvae can survive over a very long period of drying the snails (up to 5 months). The loss of water during this time exceeds over 2/3 weight of the snail tissues. The development of eggs is then prolonged through formation of a second generation of rediae, and the number of cercariae is usually lower Styczyńska-Jurewicz (1965b) showed that the eggs of fluke can complete their development in sea water with salinity of 13‰, the value exceeding that found in natural biotopes of its host. At higher salinities the number of dead eggs or with restrained development was higher but the latter retain for one month the ability to develop when transferred to fresh water. On the other hand, osmotic dehydration caused by, e.g. saccharose solutions, brings about a hinderance in development (Styczyńska-Jurewicz in litt.); non-electrolytic urea, penetrates easily into the eggs with no harm being dcne to the embryos, or even similar to the effect of sea water, it stimulates the development at temperatures lower than normal minimum temperature. Measurements of osmotic pressure in eggs of Physa, Limnea, and Tubifex (Styczyńska-Jurewicz in litt.) during their developments and at different salinities showed a constant hyperosmosis maintained probably by a larger amount of polysaccharides and fragments of proteins in the liquid surrounding the embryo.

Other type of experiment (Styczyńska-Jurewicz 1959) has proved that under natural conditions of the lake littoral, cercariae of *Diplostomum spathaceum* (Trematcda) showed an expansion exceeding considerably the range of occurrence of snail hosts, and that they can become dangerous for fish fry when the infestation is strong enough. Other cercariae, of *Opistoglyphae ranae* (Trematoda), showing a short period of activity (up to 8 hr — Styczyńska--Jurewicz 1961) and a clear negative geotaxis, due to this latter reaction can easily get in contact with the host i.e. tadpoles which, in turn, spend a considerable time cf a 24 hr cycle at the surface of water, because of a high oxygen demand and its deficiency in the deeper layers of the pond (Styczyńska-Jurewicz 1962a).

The problem of osmotic pressure was also dealt with in investigations carried out with 37 invertebrate species from brackish waters of the rocky reser-

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voirs (KLEKOWSKI in litt.). It was found that the osmotic pressure in hemo-
lymph is connected both with the origin of these species as well as with
osmotic pressure of outer environment.

Studies were also made of the effect of low temperatures on eggs and
larvae of dragonflies of Coenagrion and Lestes (Z. FISCHER 1958a, 1958b).
Coenagrion, being a typical representative of permanent ponds, hibernates
in the form of larvae, which, freezed in water, endure easily low temperatu-
res (down to — 4°C). Lestes, on the other hand, hibernates in the form of
eggs which also endure freezing (40% of eggs will hatch after freezing in
water down to — 20°C). Phases in the embryonic development of Lestes are
an adequate reflection of temperature and hydrological conditions of the ha-
bitat, especially in the period of high summer and low autumnal temperature,
but the resistance of the Lestes larvae to the drying factor is rather low.

The problem of geographical expansion of a snail, *Potamopyrgus jenkinsi*,
was the subject of separate studies. The eastern boundary of the occurrence
of this species, passes through Poland, the extension of this range seems to
be possible due to particular physiological properties. The nature individuals
survive easily changes in salinity within the limits from fresh water to 18‰,
and with stable concentration to 36‰ (DUNCAN 1967). The osmotic pressure of
hemolymph is always hyperosmotic as compared to the outer environment
within the whole range of salinities. Young animals endure easily salinity
changes up to 58‰, with no significant changes both in oxygen consumption
and in the heartbeat showing however a small maximum for average salini-
ties (KLEKOWSKI and DUNCAN 1966, DUNCAN and KLEKOWSKI 1967). The respi-
ration of matured animals depends slightly from the changes in salinity of
the outer environment within the range of lower temperatures (DUNCAN 1966),
it is somewhat higher at average salinities, similarly as in the case of mobility.
The survival is high at salinity of 34‰, but the animals reproduce intensely
at salinities around 12‰, and sporadically up to 26‰.

Trout eggs, which are able to develop at the extremely astatic osmotic con-
ditions, caused by accumulation of metabolites in the perivitelline fluid du-
ring the development occurring in the paraffin oil, were the subject of similar
studies (KLEKOWSKI and DOMURAT 1967). The osmotic pressure of the perivitel-
line fluid was found to increase then about 8 times, but it remained constant
within the developing embryo.

Describing a vast group of research concerned with astatic condition one
should mention experimental works on the resting stage in Copepoda, Cyclo-
poida. They supplied with information on behaviour of these animals over the
surface of the bottom, before the stage of dormancy is attained the way of en-
tering the mud and the way of returning to the active life (WIERZBICKA 1962),
as well as interspecies differences in this respect. Attempt was made to explain
physiological mechanisms which evoke the resting stage (WIERZBICKA and KĘ-
DZIERSKI 1964). The decrease in partial pressure of oxygen in the water is
an important factor in this process and a similar effect can be obtained with
the increase in H_2S concentration. In 5 species of astatic ponds as well as in
6 lake species, the vacuoles in the stomach of cyclops become filled with large
concentrate materials, the gut being closed with a characteristic "plug". This
plug consists of vacuoles with these materials and often with some crystals,
and in the species of astatic ponds it is usually surrounded with a thick coat-

ing. Such plugs, different in different species, can have taxonomic significance (WIERZBICKA 1966).

Analysis of lipid contents in some species which are ready for resting showed that the calorific value of cyclop is rather high on account of the high lipid content (WIERZBICKA in litt.).

During recent years the problems of biological productivity are more and more in the line of the Department work. This type of research is carried out within the scope of the International Biological Programme. Basing on the previous research concerned mainly with adaptations of aquatic animals to environmental conditions, with metabolism and osmoregulation, a new group of bioenergetic studies was initiated. The major emphasis in these investigations was laid upon the following: 1) the physiological mechanisms of the energy flow through food chains with a special attention given to these organisms and links of food chains, which play an important role in the transformation of energy accumulated, primarily by plants, in the form which is usable by man i.e., food and raw materials, 2) the bioenergetic laws controlling the growth and numbers of these organisms which complete with man or, in some other way, deplore natural resources, agricultural and animal production as well as facilitate circulation of parasites and other contageous diseases of man and bred animals.

Our particular interest was mainly concerned with these invertebrate groups which are important as food items of leading to production of fish. Energy budgets have been studied of a number of crustacean species occurring abundantly in water bodies, at the same time models of trophic types: filtrators, plankton predators, and bottom detritus-feeders. A copepod, *Macrocyclops albidus*, was studied as a typical example of predatory planktonic crustacean (KLEKOWSKI and SHUSHKINA 1966a, 1966b). Both the assimilation of food and the indices of gross and net efficiency were found to depend on the concentration of food in the habitat. Metabolism in the nauplii, copepodites, and adults revealed a considerable allometry, which correlated also with the food factor. In spite of all these differentiations, the general indices of the budget are useful for estimation of the productivity of planktonic communities under natural conditions. The species in question is a very efficient transformer of energy which converts the energy bound in the microplankton into the form available for plankton feeding fish. Numerical data of this study were employed in theoretical way to find methods of computation of productivity indices for natural populations (SHUSHKINA et al. 1968).

Similar studies were made for a filtering crustacean, *Simocephalus vetulus* (IVANOVA and KLEKOWSKI in litt., KLEKOWSKI and IVANOVA in litt.). The rates of feeding and respiration were analysed at different concentrations of food and with varying pH of water. A cumulated form of the balance has been elaborated for the whole development and for reproduction period of this species. It is noteworthy that there is a considerable decrease in food assimilation during the reproduction, brought about probably by in increased demand for particular building materials to reproduce embryos. This study together with that on predatory crustaceans form a good comparable material which permits to formulate some generalizations, concerning mainly the ecological efficiency, depending on the type of feeding and the efficiency of food assimilation.

Due to methodological difficulties especially little is known about the ele-

ments of energy budget of protozoans, although this group is rather important since it converts energy in the benthos biocenoses and in various communities of polluted waters. The studies of a predatory ciliate, *Dileptus cygnus* initiated by STACHURSKA (1970) gather the effect of density of these organisms and of their food on so-called doubling consumption rate, i.e., the amount of food energy necessary for doubling the number of infusories.

Extensive studies of energy budget were carried out on *Tribolium castaneum* (KLEKOWSKI et al. 1967). Measurements were taken of metabolism, calorific value, and chemical composition of the beetles during the development from an egg to a reproducing adult. The calorific value and chemical composition of food was also determined. The budget is given in differentiated and integrated form up to a given moment of the animal's life. This last approach permits to estimate directly from the results the significance of a given species in the energy flow through a given ecological community. A very substantial part of the results is that concerning the type of budget calculations and the variation of the efficiency coefficients during ontogenesis. The determination of the consumption rate in this species became tangible only after radioisotopes have been applied (DOMINAS et al. in litt.).

The energy budget of *Asellus aquaticus* (Crustacea) (PRUS in litt.) has different character than that above described. This species being of a great significance for biocenosis since it recuperates the energy mainly of allochtonous origin of dead plant debris, has rather poor assimilation and therefore low efficiency of the gross production (7.9–5.4). The calorific value of the body of this isopod is also low. In the vicinity of small ponds in a forest a similar role as that of *Asellus aquaticus* is played by diplopods which recuperate energy from decaying dead plant material (STACHURSKA 1968). The metabolism and survival of these arthropods depend to a greater extent on the degree of parasite infestation. Another studies of metabolism and other elements of energy budget were also started with two species of thyrogliphid mites (Acarina), which are pests to storage houses and food products (STĘPIEŃ and KLEKOWSKI in litt., KLEKOWSKI and STĘPIEŃ in litt.). In spite of what had been expected, the metabolism of these mites was found to depend only slightly from the sequence of active and resting stages of the development. It can be suggested that the negative role of these dangerous pests results mainly from contamination of the food whereas direct consumption of the food is rather moderate due to high coefficients of assimilation and conversion of energy of food into consumers biomass. Because of its significance for pest control it is interesting to add here about the work on the hormonal regulation of development in insects, and its application in controlling the population numbers. In cooperation with the Department of Biochemistry, measurements were performed of the intensity of oxygen consumption by larval stages of Lepidoptera (CZAJA-TOPIŃSKA and KLEKOWSKI 1969).

Z. FISCHER, continuing her studies on biology of dragonfly larvae, has also completed the energy budget of these insects. Larvae of Coenagrion and Erythromma are typical predators hunting from ambush (1964b), their food selection is limited and depends on how the prey moves about. The larvae of Lestes (Z. FISCHER 1966, 1967a, b), also predators, preferred the weed fauna to the plankton on account of higher calorific value of the former. This preference disappeared when the larvae were at the final stage of growth, preceding their metamorphosis in a short-lasting pond. At that time they showed

extreme voracity which accelerated their growth. Due to hemimetabolous metamorphosis the elements of energy budget did not reveal any substantial changes. The period preceding metamorphosis, although without input of energy, is not a physiolcgical famine. Relatively low amount of energy being used for respiration and a high growth rate resulted from inactive mode of life; with a very high assimilation of food the coefficients of gross production efficiency (35–25%), and net prcduction efficiency (starting from 9% during the first days to about 65% at the end of development) were also high.

A separate group of papers was devoted to detailed studies of metabolism, which is one of the most important elements, apart from biomass prcduction, of energy budget. Eudiaptomus were infested experimentally with the larvae of tapeworm, *Diphyllobothrium latum* (Klekowski and Guttowa 1968), and the oxygen consumption was measured. It was found that the parasites have affected strongly the oxygen consumption by copepods only when they were at the process of organogenesis. This indicates a high degree of adaptation in this particular parasite-host system, and also the reduced harmful interaction. Other paper of this group was devoted to the effects of temperature and oxygen concentration on survival, respiratory movements, and O_2 consumption in the larvae Perlodes (Plecoptera) and Cleon (Ephemeroptera) (Kamler 1969). The described dependences are clearly connected with properties of a normal biotope cf these species, and the respiratory movements enable regulation of the metabolism intensity under poor oxygen conditions.

The studies cf energy budget of fish aimed at characteristics of economically useful species, and especially at estimation of efficiences of food utilization for the biomass increment.

The earliest bioenergetic studies in ichthyology still continued were those of plant feeding fish (Z. Fischer 1968, in press). Food selection of grass carp, at the maximum food availability, depended mainly from mechanical structure of food, it changed with the age of the fish, on account of changes occurring in the developing mouth organ. The daily food consumption of grass carp was high, as one would expect, because of a low food assimilation (less than 2%). Similar works have been started with carp and perch. The feeding behaviour in fish was also a subject of studies carried out by Paschalski (1959b).

A separate branch of research on productivity of water bodies is that concerned with food resources. An impcrtant role in this respect is played by microorganisms as well as by suspended and dissolved organic substances. Nitrogen-fixing bacteria (E. Fischer 1960) play an important role in increasing the amount of nitrogen in astatic ponds, the intensity of these phenomena being related with the type of pond. The intensities of nitrifying and denitrifying processes do not depend directly on the number of bacteria. In other groups of bacteria (E. Fischer 1961), the abundance of microorganisms is neither an adequate indicator of their activity and production: those groups of bacteria which were most numerous in winter showed the highest activity in spring and summer, when their abundance was decreasing. An important measure of bacterial production in water and in bottom deposits of astatic ponds can be expressed by the coefficient of production efficiency, i.e. the production to biomass ratio. This index in the natural conditions, that is, when the development of the bacterial community is limited, showed

the highest values, typical for various biotopes (E. FISCHER 1961, 1966a, b, in litt., in press.). A somewhat separate problem dealt with in the Department was concerned with sulphuric bacteria in waters of a sulphur plant (E. FISCHER and DOWGIAŁŁO 1965). To this group of papers can be also included the studies on carbohydrates derived from dead plants or constituing secondary pollution of water. Those substances are easily available nutritional substrate for microorganisms, which bring about either selfpurification of water from organic compounds dissolved in it or they form themselves the particulate food for filtrators. It appears that the polysaccharide fraction is much more resistible than are mono- or oligosaccharide fractions to the action of microorganisms. In the products of bacterial decomposition of plants, other polysaccharides were found than those of the initial material which indicates that in water, similar as in soil, the microorganisms resynthetize polysaccharides (DOWGIAŁŁO 1966). In a dam reservoir, a correlation was found between the amount of chlorophyll and that of polysaccharides throughout the year, but in the astatic waters this correlation was blurred during the vernal season by the carbohydrates of allochtonous origin (DOWGIAŁŁO 1967).

Within the research on productivity of water bodies, from observations on annual dynamics of abundance, chemical composition, and calorific content of seston in dam reservoirs, fish pond, and astatic ponds of Poland and Czechoslovakia, in the cooperation with the laboratory of Dr. BLAZKA of the Laboratory of Hydrobiology of Czechoslovakian Academy of Sciences, a comparative elaboration was completed which gathered the results of several converging disciplines; namely hydrobiology, physiology, and ecology.

Recent investigations in the Department, pertaining to the problem of bioenergetics and bio-production, have found its best expression at the symposium to which this volume is devoted. Besides several factual papers (STACHURSKA, WIERZBICKA, KĘDZIERSKI), the volume comprises general elaborations on the theory of energy budgets (KLEKOWSKI), on feeding by aquatic animals (Z. FISCHER), on the significance of calorimetry (PRUS), and respirometry (KAMLER) for bioenergetic studies, on energetics of osmoregulation (STYCZYŃSKA-JUREWICZ), on the role of dispensed organic matter in waters (DOWGIAŁŁO), and on the importance of chemosynthetic bacteria in the process of recuperation of energy (E. FISCHER).

The development of such diversified studies has been possible to some extent, due the organizational bounds which unite the Department of Hydrobiology with other Departments of the Institute, especially with the Departments of Biology and Biochemistry. Mutual cooperation and stimulating consultations, often rendering the equipment materials and apparatures, all this permits to develop research methods, which being generally known and accepted are not always satisfactory for particular purposes. This is why there has been a strong tendency to develop or searching for modernization, adaptation and modification of these methods. The field equipment needed adjustment for application to a very small water bodies. Here should be mentioned the algological glass plate method, by WYSOCKA-BUJALSKA (1958a), certain apparatures for sampling and for measuring water temperature (PASCHALSKI 1959c, KLEKOWSKI 1960b). The chemical analysis of organic substances in waters, application of special methods of chromatography, methods of identification, and elimination of components disturbing the analysis (DOWGIAŁŁO 1959, 1965, 1968, DOWGIAŁŁO and FISCHER 1960), all this was faced with serious

difficulties resulting mainly from the specifity of waters examined (astatic ponds, dam reservoirs) which are considerably different from the average, better explored types of water reservoirs. The commencement of the bioenergetic studies necessiated the elaboration and adaptation, mainly miniaturization of the methods for measurements of food consumption metabolism, calorific value, chemical composition (KLEKOWSKI 1966a, 1968, KLEKOWSKI and KAMLER 1968, KAMLER 1969, PRUS 1968, DOMINAS 1968) as well as development of microbiological studies (E. FISCHER 1961, 1966a). The progress in developing and improvement of bioenergetic methods became evident at the training course of the International Biological Programme, whose part concerning invertebrates, was held in the Department of Experimental Hydrobiology in the spring 1968. Further research of the Department will follow the line of developing the experimental studies connected mainly with the physiological mechanisms of biological productivity. It is expected that the data which are being gathered at present, concerning the parameters of energy budgets of aquatic animals, especially of those species which are dominant and potential objects of economic improvement will enable to work out the principles of "comparative energetics" of these organisms. Still further the aim will be ambition to control the energy flow through simple systems consisting of several trophic levels. To seek the way of directing the energy flow through an ecosystem towards the form most advantageous for man will be the topic of the future research, e.g. the theoretical backgrounds of the introduction and stimulation of efficient transformers of energy with a simultaneous preventing the trophic resources being taken over by those ecosystem elements which do not lead to usable production.

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