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### NEW WAY OF ESTIMATE OF EFFICIENCY OF ENERGY USE IN COPEPODS DURING MIGRATIONS

#### *NOUVELLE METHODE D'ESTIMATION DE L'EFFICACITE D'UTILISATION DE L'ENERGIE SUR LA MIGRATION DES COPEPODES*

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**SUMMARY** - It is shown that the energy expenditures on the mechanical movements of copepods depend on the knowledge of character of velocity movements range at active phase. The method of direct estimates of energy expenditures for copepod' vertical migration permits to determine more real coefficients of chemical energy utilization on the mechanical work.

Nowadays problem of copepod's energetic metabolism attracts attention of a circle of investigators in connection with widespread phenomenon of diurnal vertical plankton migrations in the ocean. Numerous data on average velocity of transference of great bulk of plankton or separate species were got (Vinogradov, 1968 ; Afrikova, 1976 ; Pavlova *et al.*, 1977 ; Rudyakov, 1977 ; Rudyakov, Voronina, 1973) and great number of investigations on determination of total energetic metabolism of small crustaceans were conducted at standard experimental conditions and summarized by Winberg (1976) and Sushchenya (1972). The estimations of energy expenditures on active metabolism were also conducted (Vlymen, 1970 ; Afrikova, 1972 ; Winberg, 1976 ; Klyashtorin, Yarzhombek, 1973 ; Petipa, 1966, 1981).

Points of view of investigators were different. Some of them, (Vlymen, 1970 ; Sushchenya, 1972 ; Winberg, 1976 ; Klyashtorin, Yarzhombek, 1973 ; Klyashtorin, Kuzmicheva, 1975 ; Klyashtorin, 1978), basing on experimental study of respiration and swimming of small animals in limited liquid volumes, or, taking into account average velocities of vertical copepod's migrations in the sea, came to the conclusion that energy expenditures on active movements are small (1, 1-2 times higher than standard metabolism). Another investigators (Petipa, 1966, 1981 ; Pavlova *et al.*, 1977 ; Minkina, 1981, 1982 ; Ostrovskaya, 1976) according to direct estimation of expenditures of some substrates and body mass of animals in the period of migration or by kinematograph pictures of copepods' swimming at experimental conditions, demonstrated that expenditures of matter and energy may reach rather high meanings, 400-700 times higher than level of standard metabolism at the periods of most active movements. At an average total daily metabolism is these cases may be 6-13 times higher than standard one.

Discrepancy is in estimation of possibility of existence of energy metabolism of such high intensity. Let us show the reasons.

1) Supporters of low active metabolism do not admit existence of high swimming velocities of small plankton crustaceans. Therefore, for calculation of active or total metabolism they put in calculation formula of energy expenditures on mechanical work the average movement velocities of all population or sometimes average and the lowest of separate animals' movement velocities (Klyashtorin, Yarzombek, 1973 ; Klyashtorin, Kuzmicheva, 1975 ; Klyashtorin, 1978).

Meanwhile, nowadays reasonable data appear, proving rather higher copepods' movement velocities in the sea and under experimental conditions. Results of filming with different speed (Strickler, 1977 ; Pavlova, 1981 ; Petipa, 1981) at different conditions present precise picture of variability of swimming velocities of copepods, reaching 100- 200 cm.sec .

New methods (Petipa et al., 1977) of working with "Autoplankton BCD" (firm "Hydrobios") gave an opportunity to reveal average velocities of separate copepods' migration directly in the Sea. These velocities are 10 times higher then it was know, earlier.

Lower migration velocities marked in majority of literature source usually were calculated on the base of large periods of time between vertical hauls (from 2 to 6 hours), planned by investigators themselves.

To determine the problem of real migration velocities it is necessary to collect material in unbroken consecutive order in vertical layers at the same time with determination of environmental characteristics or also conduct in unbroken consecutive order underwater observations.

2) In most cases investigators do not know character and mechanism of copepods' natural swimming behaviour and, therefore, character of velocities change at active movement. Used average velocities do not reflect behaviour of certain animals or their separate groups, therefore, cannot be used to estimate real values and curve of movement velocities.

Behaviour and types of copepods' swimming change in dependence of their sizes, species belonging, ecological peculiarities and environments (Afrikova, 1972, 1976 ; Petipa, 1966, 1981 ; Rudyakov, Voronina, 1973 ; Enright, 1977).

All estimations of copepods' energy expenditures on mechanical work made for uniform movement with constant velocity and without stops (Klyashtorin, 1978, 1984). In nature while migration such unbroken movement without any stops don't occur?.

3) Groundless choice or approximate estimation of efficiency under transformation of chemical energy to mechanical work. Practically there are no literature data allowing to determine substantially this coefficient in copepods. Statements, numerous conditionalities and approximate or simply erroneous calculations remain in most cases at the level of suppositions and cannot reflect real values of efficiency-coefficient and its change under different swimming types with different velocities and duration of movement.

4) Use of several methods of determination of values of coefficient of hydrodynamic resistance (CHR) for enlarged, dismembered wood patterns, narcotized

or alive animals (Vlymen, 1970 ; Stepanov, Svetlichny, 1976, 1981) may influence on calculated values of energy expenditures on mechanical work. This coefficient, first of all, depends on the type and velocities of animals' swimming which are not taken into consideration in known ways of determination CHR. Approximate calculations made according to conditional models are not sufficient.

5) Very approximate or erroneous estimation of rate of oxygen diffusion in small animals (Klyashtorin, 1984 ; Winberg, 1982). It is necessary to know, however, real values of oxygen diffusion for discharge of energy expenditures determined by oxidation of energy substrates. In diffusion process dismemberment of appendages and velocity of their movement have great meaning (Waterman, 1960).

6) Use of different initial hypotheses to imagine general picture of daily vertical migration. Use of these or that concrete data and dependences and also choice of model of movements or swimming of investigated animals considerably depends on the character of accepted hypotheses. Some investigators (Stepanov, Svetlichny, 1981) made calculation of energy expenditures on mechanical work on the base of hypothesis of copepods' passive sinking to low layers and active swimming to high layers (Rudyakov, 1977). It is accepted that active movement is uniform.

However literature data and materials (Denton, 1960 ; Petipa, 1966, 1981) allow to consider that in some fishes and in plankton (in particular immigrating organisms : *Calanus* and others) as special mechanisms supported it (Hochachka, Somero, 1977). Besides, the energy expenditure on migration are more economical at neutral floatation (Pearre, 1979 ; Enright, 1977 ; Petipa, 1966, 1981).

Taking into account above-described points, as well as latest data on average and maximal velocities of copepods' migrations which are reliable enough and considerably exceed the velocities of passive sinking on corresponding species in nature, we consider hypothesis of active migrations at neutral floatation is not less reasonable than above- mentioned (Rudyakov, 1977). Knowing mechanism of copepods' rowing movement according to materials of rapid filming, new hypothesis of mechanism of copepods' migration was suggested (Petipa, 1981).

Examination of disagreements' reasons in the whole show that in most cases it appears from the lack of knowledge on given problem.

The swimming type of organisms determines the level of their energy expenditures. Can show how change of movement velocity in active phase influences the values of energy expenditures on mechanical work, we estimated quantity of energy corresponding to mechanical work performed by crustaceans in the sea during intensive vertical migrations. For this purpose two methods of calculation are applicated : in the first case we accept migration movement as periodically - uniform, in the second - as periodically - accelerated. In comparison with these methods it is submitted third method of calculation for uniform movement with constant velocity correspond to earlier mentioned notion (Klyashtorin, 1984 ; Klyashtorin *et al.*, 1973).

The formula known in physics was used :

$$A = F.v.T_A, \quad (1)$$

where : A - mechanical work, F - motive force, V - velocity of movement, T<sub>A</sub> - time of active swimming during migration, Ostrovskaya worked out mathematical

model for calculation of mechanical work in 3 showed cases outgoing from formula (1).

For first case of periodically- uniform movement formula (1) have form :

$$A = 47.6 \rho \cdot S \left(\frac{l}{\nu}\right)^{-0.56} \cdot v_c^{2.44} \cdot T_A \quad (2)$$

For second case of periodically - accelerated movement formula (1) turn into following :

$$A = ma (L_f - L_i) + 13.837 \rho S \left(\frac{l}{\nu}\right)^{-0.56} \frac{v_f^{3.44} - v_i^{3.44}}{a} \quad , \quad (3)$$

$$a = \frac{v_f - v_i}{T_A} \quad ; \quad T_A = \frac{2L_A}{v_i + v_f}$$

where:  $\rho$  - density of water,  $\nu$  - kinematic viscosity,  $S$  - area of cross-section,  $l$  - length of copepods' body,  $V_c$  - constant velocity,  $m$  - mass of body,  $a$  - acceleration,  $L_A$  - length of way,  $V_i$ ,  $V_f$  - initial and final velocities.

In both cases (first and second methods) of calculation the hypothesis on migration mechanisms of copepods described Petipa (1981) is taken into account. According to this hypothesis, sinking of crustaceans in low layers or swimming to upper layers is carried out by gradual increasing in active movement phase (i.e. between stops) of number and intensity of complex rowing acts. This hypothesis of accelerated rowing swimming is arised from results of fields observations in the Black Sea in 1975 and materials of high-rapid filming of copepods' movements in laboratory conditions.

In each separate complex rowing act "momentary" movement velocity (i.e. velocity at discrete time moment not exceeding 0.002 sec) is at first abruptly increased under strong blow of the 5 th -4 th pairs of swimming legs and then is slightly decreased under blow of 3 rd-1st pairs legs. Short period of inertial swimming follows active rows, at this time swimming legs and abdomen are brought to initial state.

In these equations are introduced the data of unbroken observations on distribution and migrations of *Calanus helgolandicus* in the Black Sea as well as the data about character of velocity change in active phase of each complex rowing act.

Character of changes of velocities in active phase of each complex rowing act according to filming data (500 stills.sec<sup>-1</sup>) is shown at table 1. This character of velocity change in active phase provides observed in the sea periodically ununiform (accelerated) swimming.

Let us divide the whole migration layer into 3 sublayers, approximately corresponding to the data of observations in the sea: 1 st layer - 30m, from 6 to 36, - 2 nd - 32 m, from 36-to 68 and 3 rd - 32 m, from 68 to 100 (Table 2). In each of them average movement velocity is regularly changed, gradually increasing to the end of the migration which was really observed (Petipa, 1981 - table 41). But average movement velocity during whole migration, taking into account stops, was 12 cm.sec. We can assume that in first sublayer to 30 m crustaceans made 4 complex rowing acts, in 32 m second - 5 and in the 32 m last sublayer - 7 rowing acts in active phase. At such distribution of rowing acts in investigated layers average migration velocity also equal to 12 cm.sec<sup>-1</sup>.

Initial parameters of crustacean movement, size and weight copepods' characteristics in the sea and got at the same time physical indices of water characteristics are presented at table 1.2.3.

The results of three methods of calculations of energy expenditures on mechanical work, taking into account character of velocity change in active phase, were compared and shown in table 4.

Conducting all necessary calculations by three methods described above we will find those energy quantities which might be expended on mechanical work by copepods in the course of migration if crustaceans moved in each migration layer periodically uniformly (1-st case), periodically hastenly (2-nd case) and uniformly without stops (3- rd case). In the first and second cases average velocity of moving copepods increased to the end of migration.

Results (Table 4) show that at the first and second methods of calculation absolute energy of mechanical work  $V$  copepodites *C. helgolandicus* (13 min of migration; 2.81) min of active movement, (Petipa, 1981) is expressed by commensurable values: in the first case- $13.2 \cdot 10^{-4}$  cal. animal<sup>-1</sup>, in the second - $20.92 \cdot 10^{-4}$  cal. animal<sup>-1</sup> (average wet body mass - 0.631 mg; 0.145 mg of dry matter; size - 0.3 cm). Results of the second method of calculation which are 1.6 times higher than first value are more real, as they reflect more exactly the character of change of movement velocity in active phase.

According to all experimental data duration of periods of active and passive states at rowing swimming is approximately identical and is equal 0.2-0.5 sec<sup>-1</sup>. Covered ways reach in active phase some cm (from 4-5 to 20) and velocity of movements changes (from 1 to 170 cm.sec<sup>-1</sup>) (Petipa, 1981; Minkina, 1981).

Table 4 presents also calculation of energy expenditures on mechanical work by third method according to Klyashtorin (1978, 1984), who used only average velocity of passing the migration layer -12 cm.sec<sup>-1</sup>. Considering the movement as a constantly uniform one during whole migration (13 min), that is, thought, not corresponding to reality, it is received the values of energy expenditures on mechanical work 5-10 times lower (up to  $2.6 \cdot 10^{-4}$  cal.animal<sup>-1</sup>) than our estimations by 1-st and 2-nd methods. Taking efficiency-coefficient equal to 0.05, we determined that under condition of short term migrations (0.023 days: swimming up and down) average for the 24 hours metabolism level does not exceed 1.3 of standard metabolism. Klyashtorin (1978, 1984) under these conditions got analogical values (1.08-1.24 of standard metabolism). Thus, slight exceed of daily metabolism over standard one, taking into account migration, can be received but only on condition of uniform movement without stops.

Now we will show how may efficiency-coefficient change under transformation of chemical energy to mechanical during swimming of copepods. It is possible to calculate this efficiency using the data of direct estimation of expenditure of body matter of copepods in the sea at migration. Direct estimation of energy expenditures is made on the same materials according to which copepods' migration was described (2-nd case).

Petipa (1981, p. 200) showed that matter expenditure in the course whole migration is uniform and losses of carbon and body dry mass form mean  $0.00202$  cal.m<sup>-1</sup> in each layer. Hence, we can determine how much energy will be spent only during active work of appendages (or active movement), if total metabolism during whole migration (13 min) is equal to 0.19 cal (Fig.1).

Total energy expenditures proportional to time of active movement in each of distinguished layers will be expressed by following meanings : in first 30 m of swimming during 1.13 min -  $16.515 \cdot 10^{-3}$  cal ; in second 32 m during 0.97 min -  $14.176 \cdot 10^{-3}$  cal and in the third 32 m during 0.7 min -  $10.23 \cdot 10^{-3}$  cal.animal .

By the same way energy expenditures on standard metabolism at the same time of active movement in each layer may be calculated. In the works (Petipa, 1966, 1981) energy expenditures on standard metabolism during whole migration period (13 min) of *V* copepodites were estimated also ( $3.14 \cdot 10^{-4}$  cal.animal<sup>-1</sup>) on the basis of direct measuring of respiration of different stages of *Calanus*, made by Marshall and Orr (1958). Average sizes of crustaceans and temperature of experiments corresponded conditions of standard metabolism (Q) from body mass (w) :  $Q = 0.00042 w^{0.81}$ . Present dependence more approaches the level of basic metabolism (Pavlova, Minkina, 1982).

“Standard” (basic) metabolism during active movement of copepods in each layer will be equal to  $2.729 \cdot 10^{-5}$  ;  $2.342 \cdot 10^{-5}$  and  $1.69 \cdot 10^{-5}$  cal.animal<sup>-1</sup> correspondingly.

Active metabolism during work of appendages (active swimming) must be equal to the difference between total and basic (or standard) metabolism at the same periods of time. In our case active metabolism is equal to  $16.488 \cdot 10^{-3}$  ;  $14.152 \cdot 10^{-3}$  and  $10.213 \cdot 10^{-3}$  cal.animal<sup>-1</sup> correspondingly.

Knowing energy expenditures on mechanical work, calculated by formula (3) (second method) we can calculate efficiency of transformation of chemical energy to “mechanical” as ratio of energetic equivalent of mechanical work to active metabolism during the same period. In each of 3 layers of migration efficiency-coefficient is equal to :

$$1/ \frac{40.774 \cdot 10^{-5} \text{ cal}}{16.488 \cdot 10^{-3} \text{ cal}} = 0.0247 \qquad 2/ \frac{68.150 \cdot 10^{-5} \text{ cal}}{14.152 \cdot 10^{-3} \text{ cal}} = 0.0482$$

$$3/ \frac{100.270 \cdot 10^{-5} \text{ cal}}{10.213 \cdot 10^{-3} \text{ cal}} = 0.0982$$

So, during copepods' migration in the sea efficiency changes from 2,5 to 10 % which are quite real and not far from being values observed also in other organism. For example, a man has efficiency of transformation of chemical energy to mechanical work equal to 22 %, humming-bird - 8 % (Alexander, 1970). Mean, during whole migration in this case efficiency turned out to be equal to 5 %. Here this value may be considered as quite reliable.

Efficiency increase to the end of migration testifies to more effective use of chemical energy under the greatest number of complex rowing acts in active phase. Moreover, the faster number of consequent powerful rowing acts increase the more effectively energy is used, though absolute energy expenditures are also increased.

Thus, estimation of energy expenditures on mechanical work at animals' movement according to certain physical laws occur to be the more right on condition that the character of velocities' change and movement mechanism are better known.

Comparison of active metabolism in *C.helgolandicus* with standard one for 3 distinguished layers confirm our previous conclusions: active metabolism in present case at migration period is 604 times as high as standard one and total diurnal metabolism is 12 times as high. The crustaceans living in upper and low layers in the periods between migrations have metabolism not higher than standard one. Presented results of determination of energy expenditures on active metabolism are the maximum ones, as they are got for migration with maximum velocities and during the shortest period. It is absolutely evident that at slower movement with low velocities the absolute and relative energy expenditures will be lower (Afrikova, 1972; Minkina, 1981).

New data about expenditures of lipids, proteins and carbon-hydrates in genus *Pleuromamma* at intensive vertical migration in the Indian ocean (Trusevich, 1985) confirm well our materials and calculations. Trusevich made hauls during 2 hours before migration start and during 2 hours after the end of migration. For migration period *Pleuromamma* spent  $0.92 \text{ cal.mg}^{-1}$  of body dry weight or it is equal  $- 0.00181 \text{ cal.m}^{-1}.\text{animal}^{-1}$  (that is in fact the same value as in *Calanus* -  $0.00202 \text{ cal.m}^{-1}.\text{animal}^{-1}$ ).

At diversity of species and their behaviour and also at presence of some types of swimming in one and the same species, different energy expenditures will be revealed. To estimate possible limits and levels of energy metabolism of copepods in the sea, new methods and further investigations of bioenergetics are necessary not only in experiments but also in natural environment. Suggested estimation of expenditure of body dry mass in copepods directly before beginning and at the end of migration, if crustaceans do not feed at this period and were not transferred by water flows, may be considered as one of such methods.

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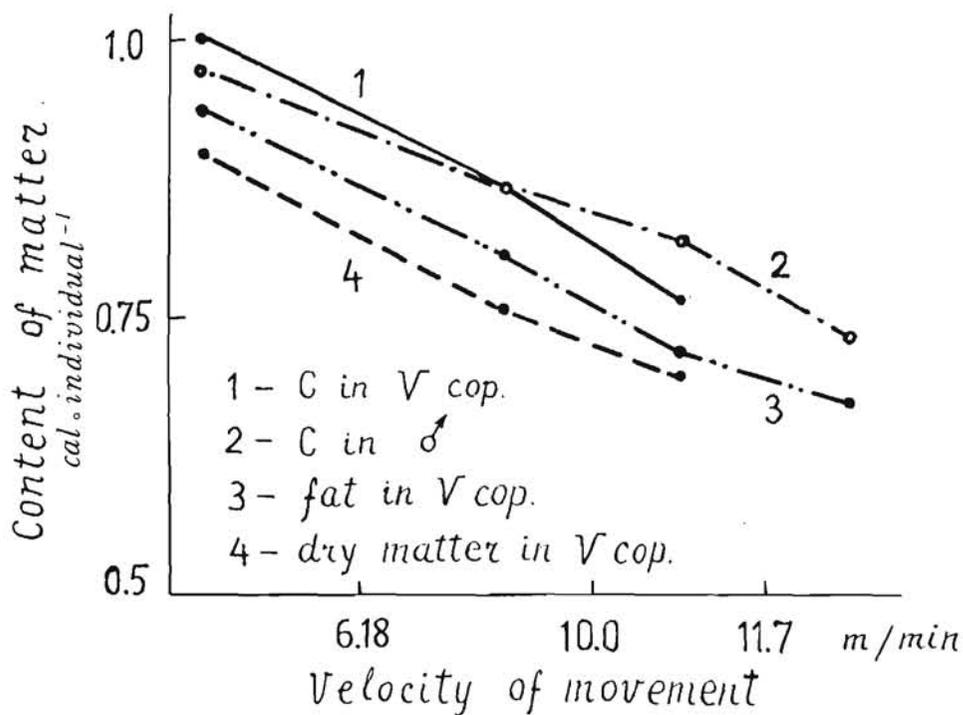


Figure 1 - Change of content of dry matter, fat and carbon in *C. helgolandicus* at different velocity of migration.

Rowing act						
1-st	2-nd	3-rd	4-th	5-th	6-th	7-th
a.						
0.0	12.0	16.0	20.0	40.0	52.5	65.0
6.5	15.0	20.0	32.5	80.0	72.5	95.0
10.0	27.0	35.0	55.0	92.5	97.5	105.0
21.5	35.7	55.0	75.0	92.5	105.0	125.0
21.5	35.7	64.0	82.5	92.5	105.0	125.0
28.5	25.0	50.0	82.5	85.0	95.0	115.0
28.5			70.0			
21.5						
b.						
14.2	20.0	35.0	55.0	75.0	85.0	100.0
10.0	16.0	35.0	40.0	65.0	70.0	90.0
10.0	14.0	25.0	35.0	55.0	55.0	80.0
	14.0	20.0	35.0	45.0	52.5	75.0
				45.0		

TABLE I - CHARACTER OF CHANGE OF MOVEMENT VELOCITY ( $\text{cm}\cdot\text{sec}^{-1}$ )  
IN *CALANUS HELGOLANDICUS* :  
a) ACTIVE PHASE OF EACH COMPLEX ROWING ACT ;  
b) INERTIAL MOVEMENT.

Layer , m	Temperature , $^{\circ}\text{C}$	Salinity , ‰	Density , $\text{g}\cdot\text{cm}^{-3}$
6 - 36	24.7	18.38	1.011
36 - 63	7.7	18.90	1.013
63 - 100	8.2	20.76	1.017

TABLE II - PHYSICAL ENVIRONMENTAL CHARACTERISTICS  
IN THE PERIOD OF OBSERVATIONS

Depth, m	Volume of copepod, mm <sup>3</sup>	Average weight , mg		Calorie indiv.	Carbon content	
		wet	dry		mg	cal
6.5	0.627	0.639	0.164 ± 0.006	0.901	98.3 ± 3.6	0.963
65	-	0.633	0.140	0.769	68.0	0.679
100	0.566	0.622	0.130 ± 0.010	0.714	79.3 ± 4.4	0.733

TABLE III - SIZE AND WEIGHT PARAMETERS IN V COPEPODITES  
C. HELGOLANDICUS IN THE PERIOD OF INVESTIGATIONS

Layer of migration , m	I method (periodically- uniform movement)	II method (periodically- accelerated movement )	III method (uniform move- ment with cons- tant velocity)
6 - 36	2.503	4.077	0.683
36 - 68	4.255	6.815	0.942
68 - 100	6.402	10.027	0.938
6 - 100	13.160	20.919	2.563

TABLE IV - ENERGY EXPENDITURES ( $10^{-4}$  CAL) FOR MECHANICAL WORK  
DURING VERTICAL MIGRATION CALCULATED BY DIFFERENT METHODS