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Study of energy balance and glycogen content in *Scolecithrix danae* (Lubbock) given various diets

by

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STUDY OF ENERGY BALANCE AND GLYCOGEN CONTENT IN SCOLECITHRIX DANAE (LUBBOCK) GIVEN VARIOUS DIETS

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When investigating the behaviour of an ecosystem, some of the most important questions are the interconnections of the food balance, the level of the energy substrate at which the equatic organisms live, and their diet. 76*

The chemical energy required for the physiological functions of the cell and the living organism as a whole is obtained from three basic food components - proteins, fats and carbohydrates. The highest energy value (efficiency) is that of fats (9.3 $kcal \cdot g^{-1}$) while that of proteins and carbohydrates is only half as great (4.1 $kcal \cdot g^{-1}$). Nonetheless the role of

*The figures in the right-hand margin indicate page numbers in the original (Tr.).

carbohydrates in the processes of accumulation, transformation and energy expenditure is quite considerable and must be taken into account when calculating energy expenditure at any biological level - from the cell to the organism and community.

Carbohydrate exchange in marine crustaceans has been the subject for investigations by a number of authors [14, 17, 19]. It has been established that there is a fairly high level of reserve glycogen and a high level of activity by glycogenolytic enzymes in the tissues of crustaceans [11]. This ind indicates a considerable use of carbohydrates and anaerobic mechanisms in energy production by these organisms. There are not a lot of such works, however, and their results are frequently contradictory.

For several species of planktonic crustaceans a relation has been demonstrated between the nature and intensity of carbohydrate exchange and the season of the year, the time of day [1, 13], the animals' stage of development [15] and type of food [20]. In the latter work it was established that the carbohydrate level in the bodies of carnivorous amphipods is higher than that in herbivorous crustaceans.

The energy balance of marine plankton has been studied for a number of species from various parts of the world's oceans. Results revealed the proportion of plant and animal sources in their food intake, the amounts of food consumed and assimilated, the daily food cycle of the organisms and so on [5, 6, 8-10, 16 and others]. A comparison of available data on the energy
balance and carbohydrate exchange of crustaceans is often impossible, however, 77
because of the great diversity of the species investigated and the different conditions under which the experiments were conducted.

The main focus of this work is a comprehensive study of the energy balance and glycogen content of <u>Scolecithrix danae</u> when restricted to various diets. It is one of the mass crustacean species in the Indian Ocean.

Material and Methods. The experiments were conducted on animals caught within the region of the first polygon (a description of the area under investigation is given in work [7]). The material was collected in DZhOM nets with an 80 cm diameter mouth, equipped with No 23 gauze (0.333 mm mesh). The small animals used to feed *S. danae* were also caught with a DZhOM net fitted with No 49 gauze (0.112 mm mesh).

The animals in the experiment were examined after 12 hours of adaptation to the type and quantity of food offered them. The crustaceans were kept in litre jars in filtered sea water to which three types of food had been added - animal, vegetable and mixed. The animal food was provided by *Oncaea* sp. in concentrations of 9.6 $cal \cdot l^{-1}$, the vegetable source by the unicellular algae *Gymnodinium lanskaya* in concentrations of 4.0 $cal \cdot l^{-1}$. The mixed food consisted of *G. lanskaya*, phytogenic detritus in amounts of 0.5 $cal \cdot l^{-1}$ and *Oncaea* sp. - 1.0 $cal \cdot l^{-1}$. The concentrations and types of mixed food in the experiments were selected on the basis of previously determined amounts of phytoplankton (L.M. Sergeeva), microzooplankton (our data), and zooplankton (E.V. Pavlova) from the accumulation layers of the seston. The conditions under which the food specimens were kept and prepared are described in the article by T.V. Pavlovskaya and G.I. Abolmasova [4]. The energy equivalent to the body mass of the crustaceans and their food was determined by the wet combustion method with a 15% correction for incompletely oxidized organic matter [3]. The energy equivalent for the body mass of *S. danae* constituted 0.94 $cal \cdot sp^{-1}$, the fresh weight - 0.85 $mg \cdot sp^{-1}$.

The energy balance of the animals was studied using the radiocarbon method [12]. A detailed description of the method for these experiments can be found in the article by T.V. Pavlovskaya, and G.I. Abolmasova [4]. The glycogen content in the tissues of the crustaceans was determined by the enzymatic method [18]. The analysis and the treatment of the tissues were carried out under the necessary refrigerated conditions.

The number of animals in the experiment vessels and the exposure time varied with the type of work being done. The energy balance was studied on the basis of 8-14 specimens, the glycogen content on the basis of 25 specimens. In the energy balance experiments on the tagged food, the exposure time varied from 0.5-1.5 hours depending on the type of food and the time of day, in the glycogen experiments it was 24 hours. The daily values for the elements in the food balance of the animals were obtained from the appropriate source components determined in short experiments conducted both day and night. The change in the amount of glycogen in the body of the crustaceans over the course of the experiment was determined by the difference between its content in the control sample and after the animals had been exposed to the various types of food for 24 hours. The control sample consisted of organisms caught from the same body of water before the experiment. Each series of experiments consisted of three repeats, the water temperature in the vessels was 21-22°C.

Results. Energy balance and glycogen content in copepods restricted to plant food. Experiments to determine the elements of the energy balance of *S. danae* when restricted to the unicellular algae *G. lanskaya* showed (Table 1) that the rate of food consumption was similar both day and night. On the other hand the assimilability of the algae was lower in the day than at 79
night, constituting 0.17 and 0.41 respectively. The relationship between the energy accumulated in the body (C_d) and that expended on respiration (R_c) remained practically unchanged throughout the whole 24 hour period. The bulk of the assimilated algae was expended on respiration. Liquid excreta (R_d) accounted for from 23.4 to 40.0 of the total unassimilated energy (F). With this type of food the daily intake of the copepods was very low constituting 0.9% of the body mass.

Таблица 1

Показатели энергетического баланса у S. danae в разное время суток при потреблении одноклеточных водорослей

Время суток 1	Число животных в опыте 2	$C_r \cdot 10^{-6}$ кал×хим$^{-1}$ 3	$C_d \cdot 10^{-4}$	$R_c \cdot 10^{-4}$	$R_s \cdot 10^{-4}$	$R_d \cdot 10^{-4}$	$A \cdot 10^{-4}$	$C \cdot 10^{-4}$	σ_A	σ_C	a	σ_a	$\frac{C_d}{A}$	$\frac{R_d}{F}$	$A_{сут}$ 5	$C_{сут}$ 6
			кал·экз$^{-1}$·12 ч$^{-1}$ 4										%		% энергетического эквивалента массы тела 7	
День 8	8	8,45	0,9	2,6	12,6	19,3	3,5	35,4			0,10		26,5	60,5		
	10		3,6	4,4	25,8	32,0	8,0	65,8			0,10		44,5	55,4		
	10		0,9	6,7	13,6	0,6	7,6	21,8			0,30		11,7	4,2		
Среднее 9			1,8	4,6	17,3	17,3	6,4	41,0	1,4	13,0	0,17	0,07	27,6	40,0	0,3	0,9
Ночь 10	10	8,45	11,7	15,2	21,3	1,6	26,9	49,8			0,54		43,4	39,3		
	13		7,5	9,9	35,3	0,8	17,4	53,5			0,32		43,0	16,3		
	14		8,3	10,9	29,4	0,6	19,2	49,2			0,39		43,1	14,7		
Среднее 11			9,2	11,7	28,7	1,0	21,2	50,8	2,9	1,3	0,41	0,06	43,2	23,4		

C_r — удельная активность корма, C_d — накопление энергии в теле, R_c — траты на дыхание, R_s — фекалии, R_d — жидкие экскреты, A — усвоенная пища, C — потребленная пища, a — усвояемость, F — суммарное неусвоенное вещество.

Таблица 2

Показатели энергетического баланса у S. danae в дневное (над чертой) и ночное (под чертой) время суток при потреблении смешанного корма

Вид корма 1	Число животных в опыте 2	$C_r \cdot 10^{-6}$, кал×хим$^{-1}$ 3	$C_d \cdot 10^{-4}$	$R_c \cdot 10^{-4}$	$R_s \cdot 10^{-4}$	$R_d \cdot 10^{-4}$	$A \cdot 10^{-4}$	$C \cdot 10^{-4}$	σ_A	σ_C	a	σ_a	$\frac{C_d}{A}$	$\frac{R_d}{F}$	$A_{сут}$ 5	$C_{сут}$ 6
			кал·экз$^{-1}$·12 ч$^{-1}$ 4										%		% энергетического эквивалента массы тела 7	
G. lanskaya 8	15 / 13	12,9 / 8,45	1,1 / 4,2	3,6 / 7,9	4,1 / 5,9	1,3 / 2,8	4,7 / 12,1	10,1 / 32,6	0,6 / 1,5	1,6 / 7,1	0,50 / 0,39	0,11 / 0,06	23,9 / 33,6	21,2 / 12,2	0,2	0,4
Детрит 9	13 / 13	44,0 / 44,0	25,7 / 16,9	24,4 / 10,6	19,0 / 43,2	0,7 / 5,3	50,1 / 27,3	70,1 / 76,0	9,0 / 6,3	13,4 / 9,8	0,72 / 0,40	0,03 / 0,09	51,8 / 57,5	3,6 / 10,6	0,8	1,4
Oncaea sp. 10	13 / 13	860,0 / 860,0	76,0 / 20,8	213,6 / 227,2	172,0 / 447,2	89,6 / 27,2	292,5 / 247,7	553,0 / 772,3	2,1 / 39,0	55,0 / 190,0	0,54 / 0,38	0,05 / 0,09	26,6 / 10,6	26,9 / 8,3	5,5	13,2
Сумма 11			102,8 / 41,9	241,6 / 245,7	195,1 / 496,3	91,6 / 35,3	54,8 / 287,1	634,1 / 880,9							6,5	15,0

Tables 1 & 2.

Table 1. Indices for the energy balance of *S. danae* at various times of the day when fed on unicellular algae

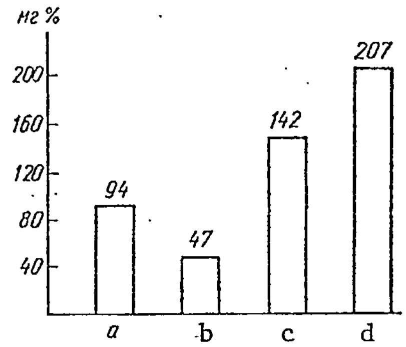
1. Time of day
2. Number of animals in experiment
3. $C_r 10^{-6} cal \times imp^{-1}$
4. $cal \cdot sp^{-1} \cdot 12\ hr^{-1}$
5. $A_{24\ hr}$
6. $B_{24\ hr}$
7. Body mass as % energy equivalent
8. Day
9. Average
10. Night
11. Average

C_r - specific activity of food, C_d - energy accumulation in body, R_c - expenditure on respiration R_s - feces, R_d - liquid excreta, A - food assimilation, C - food consumption, a - assimilability, F - total unassimilated matter.

Table 2. Indices for the energy balance of *S. danae* during the day (above the line) and at night (below the line) with consumption of mixed food.

1. Type of food
2. Number of animals in experiment
3. $C_r\ 10^{-6}$, $cal \times imp^{-1}$
4. $cal \cdot sp^{-1} \cdot 12\ hr^{-1}$
5. $A_{24\ hr}$
6. $C_{24\ hr}$
7. Body mass as % energy equivalent
8. *G. lanskaya*
9. Detritus
10. *Oncaea* sp.
11. Total

When the entomostracans were restricted to a vegetable diet for 24 hours a substantial decrease in glycogen reserves was observed (from 94 mg% in the control to 47 mg% fresh mass in the experiment) in the body of the animals (diagram, a and b). This indicates that at this rate of food intake glycogen is being broken down faster than it can be resynthesized.



Содержание гликогена (мг% сырой массы) в теле S. danae в условиях различных режимов питания:
а — контроль, б — растительная пища, в — смешанная пища, г — животная пища.

Glycogen content (mg% of raw mass) in body of S. danae under various diets

a - control, b - plant food, c - mixed food, d - animal food.

Energy balance and glycogen content in copepods restricted to mixed and animal foods. Experiments on the contents of the animals on the mixed diet showed (Table 2) that S. danae consumed all the types of food affered, but that the rates at which the animal and vegetable foods were consumed were very different. Thus the total daily intake of phytogenic food including live algae and detritus constituted 1.8%, while the intake of animal food constituted 13.1% of the body mass.

The plant detritus was consumed at a slightly greater rate than the live unicellular algae. This can obviously be explained by the small size of G. lanskaya (10-12 microns) and the more accessible form of the detritus which consisted of aggregations. The assimilability of the algal and animal food changed very little in the course of the day (0.39-0.50 and 0.38-0.54 respectively). There was a more significant change in assimilability with detritus consumption (0.40 at night and 0.72 during the day). The proportion of the individual elements in the balance was fairly constant over the course of the day and only changed within a few percent. When the unicellular algae and animal food were being consumed the greater part of the assimilated energy was expended on the respiration of the copepods (66.4-89.4%). With detritus consumption the values for the energy accumulated in the body and expenditure on respiration were approximately the same.

In the experiments with mixed food there was an increase in the glycogen content after 24 hours up to 142 mg% of the fresh mass as opposed to 94 mg% in the control (diagram, a, c). Unlike the experimental variant with the vegetable based food, where the intake was very low (0.9% of the body mass) and a breakdown of glycogen was observed, in this case the addition of animal food to the diet led to a predominance of processes of carbohydrate resynthesis resulting in a higher level of reserve glycogen.

As can be seen on the diagram (see figure d) crustaceans fed on high concentrations of animal food, like those on mixed food, revealed an accumulation of reserve glycogen. In the latter case, however, the value for the increase in glycogen was more than 100% greater than in the control group, obtaining 207 mg% of the fresh mass.

Discussion. The data obtained demonstrated that under natural conditions the glycogen level in S.danae fluctuates from 86 to 210 mg% of the fresh mass (Table 3). These values correspond with data in the literature for mysids (80-150 mg%) [19] and for Calanus helgolandicus (275±62 mg%), but it is slightly lower than for Pseudocalanus elongatus (134-406 mg%) [1]. The absolute values for glycogen concentration in these crustaceans is quite considerable (100-300 mg% of the fresh mass) and are comparable with data obtained on fish [2]. But the relative values for glycogen content in the experimental animals were quite small, constituting 0.3-2.2% of the body mass.

Таблица 3

Содержание гликогена у ракообразных в естественных условиях и количество ассимилированной пищи в эксперименте

Вид животного 1	Размер, мм 2	Энергетический эквивалент массы тела, кал×$\times$экз$^{-1}$ 3	4 Содержание гликогена		Ассимилированная пища, % массы тела 5
			мг % a	% массы тела b	
Scolecithrix danae	2,15	0,938	86—210	0,3—0,9	6,6
Euchaeta marina	3,26	1,095	88	0,3	32,0
Pleuromamma abdominalis	4,40	1,771	118—282	0,3—0,65	35,0
Euchirella curticauda	4,05	3,647	81—279	0,1—0,3	20,5
Cypridina serrata	2,10	0,536	74—323	0,6—2,2	31,3

Table 3. Glycogen content in crustaceans under natural conditions, and quantity of food assimilated in experiment.

1. Species
2. Dimensions, mm
3. Energy equivalent of body mass, cal x sp^{-1}
4. Glycogen content, a - mg%, b - % of body mass
5. Assimilated food, % of body mass

The results of the investigation lead us to conclude that diet (the quality and quantity of food) determines the levels of accumulated and consumed energy, and of reserve glycogen as one of the energy substrates. A close correlation has been observed between the values for indices in the energy balance and glycogen content. For the S. danae restricted to a plant diet, for example, the daily food intake was minimal (0.9% of the body mass) and the amount of glycogen was below the control level (47 as opposed to 94 mg%). In our opinion these data indicate that the type of food offered (the small algae G. lanskaya) was consumed by the crustaceans in very small quantities and that they had to draw upon reserve glycogen to supply their needs for energy. The rate at which the glycogen was consumed was considerably higher than the rate at which it was being replenished. This is reflected in the lower level of reserve glycogen. This overdraw on reserve glycogen can be partially explained by the lack of adequate access to energy substrates, to glycogen in particular, from the food.

Under natural conditions S. danae and the other crustaceans investigated do not exhibit such a low glycogen concentration as those in the plant food experiments (Table 3). This may indicate that in the region of the ocean studied plant food (small phytoplankton) is not a characteristic source of food for S. danae and that the consumption of this type of food alone would not ensure a sufficiently high level of reserve glycogen or the food needs of the organisms. The animals were starving.

On the other hand, the S. danae restricted to mixed and animal food are characterized by higher indices for the elements of the energy balance and a higher concentration of glycogen compared to that of the natural control group. The value for the daily food intake increased from 0.9% of the body mass for the S. danae on plant food to 15% of the body mass for those on mixed food. The amount of glycogen also increased - from 47 to 142 mg%. The increase in the daily intake and glycogen concentration in the body of the crustaceans restricted to mixed, or even more so to animal food (up to 207 mg%) demonstrates that feeding on animal food is more efficient and that small animals are the main source of food for the species investigated.

Like the daily intake, the amount of assimilated energy in the various
species of crustaceans which feed on mixed food is directly linked to the amount 8
of reserve glycogen. We noted no significant interspecies differences in glycogen content or the amount of assimilated energy in the five species studied (Table 3). S. danae is an exception, for which the amount of assimilated energy (6.6% of the body mass) was lower than for the other animals. We attribute this to a difference in the concentration of animal food in these experiments [4].

An analysis of the data obtained thus indicates that under the most favourable feeding conditions for S. danae reserve glycogen is accumulated, whereas in less favourable conditions the expenditure of glycogen on physiological functions is not compensated for by its resynthesis. Consequently, under certain conditions the glycogen level in the bodies of a group of animals is apparently an indirect indicator of the rate of food consumption and assimilation.

The range of fluctuation in the level of reserve glycogen of S. danae in nature leads us to conclude that the values for consumed and assimilated food obtained in the experiment with mixed food are characteristic of this species and of the natural conditions in this particular region. The sometimes very high glycogen concentrations (210 mg%) noted for this species in nature, however, indicate that higher values for food consumption and assimilation are possible for this species. This has been observed quite frequently in layers with high concentrations of seston.

This work is a part of greater iniatory efforts to study the interrelation between basic components of the food balance of aquatic animals, the most important physiological and biochemical parametres, as well as the physical and biological factors of the environment. It is hoped that it will be of future use to evaluate the productivity of various regions of the ocean.

In the future the daily and seasonal changes in these indices should be established for animals at various stages of development in areas of the world's oceans with various levels of productivity.

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STUDY OF ENERGY BALANCE AND GLYCOGEN DYNAMICS IN SCOLECITHRIX DANAE (LUBBOCK) UNDER CONDITIONS OF DIFFERENT FOOD REGIMES

Summary

It is shown that in Scolectihrix danae food regime (food quality and quantity) determines the levels of assimilated and consumed energy as well as of reserve glycogen. Feeding of the animals with vegetable diet only (unicellular alga Gymnodinium lanskaya) resulted in low diet values (0.9% of the body mass energy equivalent) and in a decrease of reserve glycogen to 47 mg% as compared with natural one (91 mg%). On the contrary, when feeding copepods with animal and mixed food consisting of unicellular algae, phytogenous detritus and Oncaea sp., the daily diet and glycogen concentration increased up to 15% of the body mass and 142 and 207 mg%, respectively.