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The elements of energy balance of the amphibiontic amphipod Orchestia bottae M.-EDW. (Amphipoda-Talitroidea)

By L.M. Sushchenya

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The Elements of Energy Balance of the Amphibiontic Amphipod Orchestia Bottae M.-Edw. (Amphipoda - Talitroidea).

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(From: "Biologiya Morya" /Marine Biology/, Vol. 15, pp. 52-70, 1968).

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The majority of the representatives of the superfamily Talitroidea (Bulycheva, 1957), to which belongs also the presently discussed species Orchestia bottae M.-Edw., achieved the ability through a number of specific adaptations in the process of evolution, to leave the aquatic medium and to go onto the land. A number of authors, in particular A.S. Pears (1950), believe that for this the main prerequisite was primarily the favourable ecological situation: vacant space, abundance of unutilized food and absence of enemies. Contemporary representatives of talitrids are adapted in various ways to life on the land. Some species have adapted themselves completely to life conditions on the land and have penetrated far inland, becoming denizens of humid forests up to the high-mountain regions. Other species, although having left the aquatic medium and having adapted themselves to existence on the land, have settled near water bodies and maintain connection with the latter. The common characteristic of these and other species is the utilization of the huge resources of decaying plant material accumulated on the land, as forest litter, or on the shores of water bodies, as stratifications of macrophytic refuse. This factor determines the importance of studying the role played by orchestia in the conversion of substance and energy within ecosystems.

The determination of the main elements of the animal's energy balance is a necessary step in the study of the above: determination of the total amount of energy consumed by the animal together with the food; determination of energy spent on respiration, on growth, and determination of energy in non-assimilated food excreted by the animals into the outside medium and returned to the biotic cycle.

One species of the talitrids, Orchestia bottae, was selected for the study. This species forms numerous populations in the supra-littoral zone of the Black Sea and is the main consumer of the macrophytes: cystozirae *), enteromorphs, sea lettuce and certain other algae. /53

Data and Methodology.

For a period of three years (1962-1965) the populations of orchestiae were regularly studied in the Golubaya Bay and in the Omega Bay near Sevastopol; in the Karadag region collections of material were carried out episodically.

After selection of samples from macrophytic refuse, the animals were divided into size-groups by means of a soil-screen, then counted, measured and weighed. The distance from the front edge of the head to the tip of the exopodite of the third uropod (without terminal setae) was taken as the body length. Both the wet and the dry weights of the crustaceans

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* TR: correct spelling of "cystozirae" is unknown to the translator.

were determined. The samples were kept until constant dry weight was achieved in a thermostat at a temperature of 100-105 ^{o}C. As a result of 1700 weighings and measurements a ratio was established of the body length to the animal's weight, as well as a ratio of their dry to wet weight.

The calorific value of the animals was determined by three methods. The main determinations (study of the dynamics of the calorific value of all the size-groups during the course of a year) were carried out by the method of bichromate oxidizability, which is extensively utilized in hydrobiology (Vinberg and others, 1934; Sushchenya, Vetrova, 1957; Sivko, 1960; Sushchenya, 1961; Ostapenya, Sergeyev, 1963). Oxidation was carried out by means of bichromate potassium ($K_2Cr_2O_7$) in the presence of a catalyst (Ag_2SO_4). The amount of oxygen required for oxidation of the batch (4 to 6 milligrams dry substance) was converted to calories counting 5 calories per one milliliter of oxygen.

The second method was direct calorimetry. This method was mainly used in the bichromate method as a control of the oxidation degree of the organic substance. Calorimetric installation UK-2 with a self-packing bomb SKB-52 is utilized in direct calorimetry (Drozdov, 1962). This installation gives good results for a batch-size ranging between 700 and

1500 milligrams dry substance. At least three combustions were carried out for determination, by this method, of the calorific value of a given animal group.

In 10 samples the calorific value was calculated by means of a third method: by chemical composition of animals.* Below, we present only generalized data on the calorific value of orchestiae. This problem is studied in detail in another work (Sushchenya, Abolmasova, in the present compendium). The ash-content of crustaceans was determined at the same time as the calorific value.

The majority of determinations are carried out through combustion of material in a muffle furnace. Some of the data are obtained from ash-remains after combustion of samples in a calorimetric bomb. /54

Respiration of animals was studied both under aquatic, and under atmospheric conditions. Atmospheric respiration of orchestia was determined by means of Dixon's differential

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* Determination of the chemical composition of orchestia was carried out, upon our request, by professor Z.A. Vinogradova at the laboratory of the Odessa branch of the Institute for the Biology of Southern Seas of the Ukrainian SSSR Academy of Sciences.

micro-respirometer (Dixon, 1943). Aquatic respiration was measured in closed vessels by Winkler's method. Depending on the size, from a few to 30-40 crustaceans participated in each experiment. The animals were preliminarily kept under laboratory conditions at a temperature close to the temperature of the experiment ($20 \pm 2^{\circ}C$). The derived data are converted to $20^{\circ}C$ by means of corrections calculated according to the "normal curve" of Krog (Vinberg, 1956). During the preliminary keeping, the animals were permitted to remain in the water or to leave it and enter the refuse layer in the aquarium. It should be noted that orchestia cannot remain in water for a prolonged period of time. If they are forced to stay in water, they perish in two-three days.

Feeding was studied in various size-groups of animals. The latter were kept on cystozira taken from the refuse layer. The rate of filling and emptying of the intestines in the crustaceans was determined, together with the content of intestines (according to the length and diameter of the latter), and the number of times the intestines were filled during a 24-hour period, weight of excreted feces after a single filling and in a 24-hour period, calorific value of food and of feces, and other data.

To study growth, several groups were selected which consisted of newborn juveniles and of animals of larger dimensions. They were placed in glass aquariums filled up to one quarter or to one fifth with algae from natural habitats of the animals. The wet and the dry weights were determined prior to the experiment. Later, the crustaceans were weighed every 10 hours, while larger animals were weighed somewhat less frequently, and the average increment was determined for the given period. The tests were carried out at a temperature of $20 \pm 1.0^{\circ}C$.

All the above-indicated data served as the basis for quantitative characteristics of a conversion of the substance and energy in the orchestia population and for the determination of the annual energy flow in the latter (Sushchenya, 1967), as well as for the calculation of elements of the energy balance in various size-groups of animals. These calculations permitted a determination of the role of the talitrid on the phytogenic beaches of the Black Sea and of the possible participation of the talitrids in the conversion of the organic substance in the littoral zone of the sea.

Observation Results.

Correlation of the dimensions, wet and dry weights in orchestia. All the animals were divided into nine size-groups at intervals of 2 millimeters: from 2 to 18-20 millimeters. Individuals of the last group occurred seldom in the population.

The empirical points reflecting the ratio of the /55
dry weight of crustaceans to their dimensions show a distinctly pronounced hyperbola (Fig. 1) on the graph.

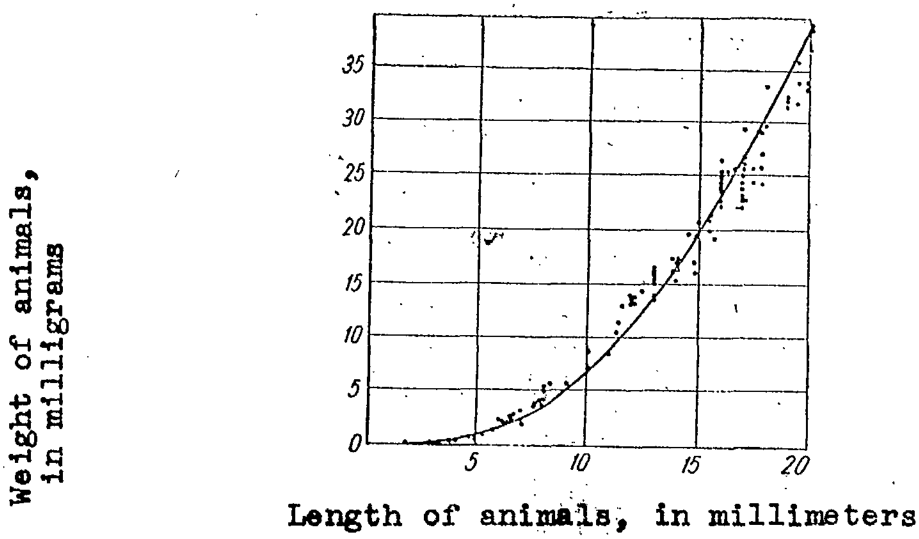

Figure 1. Change in the dry weight of O. bottae in relation to the body length.

In the system of logarithmic coordinates this is a straight line with the following equation:

$$W = 0.121 \ l^{2.75} , \qquad (1)$$

where W is the dry weight of the animals (in milligrams), l is the body length (in millimeters). We see from the obtained equation that the weight is connected to the body length by a relation raised to a power close to three.

Processing of the weighing results shows that the water content in the orchestia body is actually a constant value. The dry weight of crustaceans, regardless of their age, constitutes 32.4% of the wet weight. The correlation of these values may be expressed by the following simple equation:

$$W = 3.09 \ W_1 , \qquad (2)$$

where W is the wet weight of the animals, and W_1 is the dry one (in milligrams).

Calorific value and ash-content of the orchestia body. The calorific value of individual size-groups of orchestia was relatively stable during the course of the year and did not deviate from the average value more than 20% (Sushchenya, Abolmasova, in the present compendium). In the majority of instances these deviations did not exceed 10%. The monthly average calorific value of the animals fluctuated between 4.51 and 5.06 kilocalories, while the average for the entire population was 4.70 kilocalories per one gram dry weight per year. Its change in relation to the size of the animals, and consequently also in relation to the age of the latter, is insignificant. The mean annual values for various size-groups were within the range of 4.4 to 4.9 kilocalories per gram. They were lowest in the case of the juveniles (4.40 to 4.67 kilocalories per gram). The calorific value of animals of medium and large dimensions attained 4.9 kilocalories per one gram dry weight.

The ash-content of orchestia fluctuates within the range of 18.5 to 25.7%. The annual average, for the entire population, of the ash-content is 20% dry weight of the animals.

Feeding and daily rations of orchestia. As mentioned previously, the orchestiae live in refuse in the supra- /56
-littoral zone and are consumers of decaying plant remains. These animals have a gnawing buccal apparatus. Analysis of intestinal content and experimental studies showed that the orchestia devours mainly the cystozirae, enteromorphs and sea lettuce. They settle rarely and in very small numbers in the

eelgrass refuse, therefore, the latter is hardly consumed by them. Together with the remains of algae one often finds, in the intestines of the crustaceans, hyphae of lower fungi and a considerable quantity of bacteria. On the whole, the content of intestines in orchestiae does not differ from the composition of the substratum of the decaying algae upon which they live. The animals use not only the heavily decomposed, but also fresh algae recently thrown ashore. They consume soft portions of the thalluses.

Ninety experiments were carried out to determine the filling and the elimination rate of orchestia's intestines, as well as to determine the volume of the food lump and of the weight of emitted feces. The experiments were carried out at a temperature of 21 to 26 ^{o}C. The calorific value of the consumed algae (approximately 1.2 kilocalories per one gram wet weight) and of the feces (0.834 kilocalories per one gram of wet weight) was determined.

It was established that the animal fills and empties its intestines on an average 12 times every 24 hours. The filling and the elimination periods of the intestines are identical, on an average <u>one hour</u> long (the fluctuation is within the range of 0.5 to 2 hours). To determine these values, the animals with recently eliminated intestines were placed in crystallizers with food and kept there until the intestines were filled. Then they were immediately transferred into another crystallizer with moist cotton wads as substratum, but without any food. Here the time for the elimination of the food lump from the intestines was determined. Thus, by disrupting the feeding process artificially, it was possible to establish the length of both elements of the feeding cycle. On the basis of the experiments, we may claim that the feeding process is practically continuous: breaks in the food lump, other conditions being normal, were very seldom observed the intestines being fully filled with food all the time. The number of intestinal fillings per 24-hour period (n) may be determined approximately from the average filling time, while the weight of the food per one such filling (p) may be determined from the volume of the intestines (under condition that the specific gravity of the food is 1 /TR: "el" not "one"/). According to these data, the orientation value of the daily ration (P) may be easily determined:

$$P = np. \qquad (3)$$

24-hour-long experiments were carried out on adult animals of one weight-group (83.5 to 90.6 milligrams wet weight). Results of these experiments are shown in Table 1. In accordance with the obtained data, the daily ration of these animals is 48.4 to 77.3% of the body weight. The amount of feces isolated during a 24-hour period fluctuates within a range of 38.0 to 69.2% (on an average 48.5%) of the weight of the consumed food. We calculate the food assimilation from the difference between the calorific /57 value of food and of the feces. This difference is 30.4 to 57.7% (on an average it is 40.2%).

Table 1

Results of 24-hour-period experiments on orchestia feeding

Number of the animal	Wet weight of the animal, in milligr.	Wet weight of food per 24 hr.		Wet weight of feces per 24 hr.	
		Milligrams	% of body weight	Milligrams	% of food weight
19a	83,5	58,20	69,7	26,35	45,2
14	75,6	60,12	70,2	31,20	51,9
10	87,5	42,36	48,4	18,10	42,7
19	89,6	69,36	77,3	26,30	38,0
2	90,6	47,52	52,4	32,90	69,2

We have also conducted a considerable number of 2 to 4-hour-long experiments to determine feeding during the daylight period (mainly from 9 a.m. to noon). The obtained results, taken as averages for animals close in weight and converted to 24-hour periods, are shown in Table 2.

Table 2

Results of short-term experiments on feeding of orchestia

Wet weight of the animal, milligr.	Daily ration: Milligrams	Daily ration: % of animal weight	Feces: Milligrams	Feces: % of the ration	Feces: % of the animal's weight	Calorific value of consumed food, cal.	Calorific value of feces, calories	Assimilation: Calories	Assimilation: % of the ration
9,2	3,12	33,9	2,00	64,2	21,8	3,75	1,67	2,08	50,6
10,5	5,26	50,0	4,45	84,6	42,4	6,32	3,71	2,61	41,3
11,4	5,40	47,4	4,39	81,2	39,5	6,48	3,66	2,82	43,5
12,4	4,56	36,8	3,61	79,0	29,1	5,47	3,01	2,46	45,0
14,1	4,94	35,0	4,19	86,6	29,8	5,92	3,50	2,42	40,8
15,2	4,66	30,7	3,94	84,6	26,0	5,60	3,29	2,31	41,2
20,0	6,21	31,0	5,34	86,0	26,7	7,45	4,45	3,00	40,3
25,4	8,85	34,8	8,00	90,5	31,5	10,60	6,67	3,39	32,0
34,4	8,43	24,5	7,63	90,5	22,2	10,10	6,36	3,74	37,0
35,7	9,58	26,8	8,89	92,7	24,9	11,50	7,41	4,09	35,6
45,0	11,60	25,8	11,00	94,8	24,4	13,90	9,16	4,74	34,1
55,0	13,33	24,3	13,30	100,0	24,2	16,00	11,12	4,88	30,5
60,0	14,50	24,2	13,70	94,5	22,8	17,40	11,44	5,96	34,3
61,7	15,80	25,6	15,50	97,9	25,1	19,00	12,90	6,10	32,1
63,0	14,75	23,4	14,10	95,5	22,4	17,70	11,75	5,95	40,4
68,0	12,00	17,5	10,00	83,2	14,7	14,30	8,36	5,94	41,6
70,7	14,40	20,4	13,30	93,0	18,9	17,30	11,15	6,15	35,5
76,6	16,00	29,0	15,75	98,5	20,6	19,20	13,14	6,06	31,6
77,9	16,50	21,2	16,50	100,0	21,2	19,80	13,78	6,02	30,4

Animals weighing from 9 to 78 milligrams were used for the experiment. The daily ration (like in the preceding case, the cystozira served as food) constituted /58
17.5 to 50% of the body weight. The amount of emitted feces attained 64 to 100% of the weight of the consumed food. Having converted these values to calories, we have the amount of assimilated energy from the difference between these values. This amount of energy equals 30.4 to 50.6% (on the average approximately 35.4%) of the energy of the consumed food. Thus, the assimilation value, obtained in the short-time experiments, turned out to be close to the assimilation value of food in the 24-hour experiments.

The values presented here are important for an estimate of the consumption and of the degree of assimilation of food by the orchestiae. We may take, as a rule of thumb, that the orchestia assimilates approximately 1/3 of the consumed food.

It should be noted that a study of changes in the ration with fluctuations in the food supply in the medium is of no importance in the case of orchestia, because the orchestia, in the nature, lives almost constantly under conditions of food excess.

<u>Respiration of orchestia</u>. The given species of orchestia is well-adapted to respiration under atmospheric conditions. Its level of aquatic respiration is considerably lower than the atmospheric one (Ivlev, Sushchenya, 1961). We will discuss here the atmospheric respiration only, since its value is a necessary parameter in the determination of the energy balance of the animals.

Insofar as under standard external conditions the respiration intensity is a function of the animal weight (Weymouth and others, 1944; Zeuthen, 1947; Vinberg, 1950; Waterman, 1960), we carried out experiments with animals of various weight (dry weight of crustaceans fluctuated within the range of 0.1 to 37.0 milligrams).

According to the mentioned authors, the relation of the respiration intensity of the crustaceans, as well as of other animals, to their individual weight is expressed by the following power equation:

$$Q = AW^k, \qquad (4)$$

where Q is the oxygen consumption rate (milliliters per hour),
W is the weight of the animal (grams), A and k are coefficients. The given function is linear when logarithms are taken.

Figure 2 shows results of measurements of the respiration rate of orchestia at 20 °C in an atmospheric medium. The straight line characterizing the respiration in relation to the weight of the animals is drawn in correlation to the values of coefficients A and k calculated according to the method of the least squares.

The corresponding equation of the parabola for the given relation is expressed in a numerical form in the following manner:

$$Q = 0.56\ W^{0.74} . \qquad (5)$$

This equation enables us to calculate the respiration intensity of an animal of any weight at 20°C. Dry weight of orchestia was used for derivation of the equation. This equation has the following appearance for the wet weight of the animals; /59

$$Q = 0.243\ W^{0.74} . \qquad (6)$$

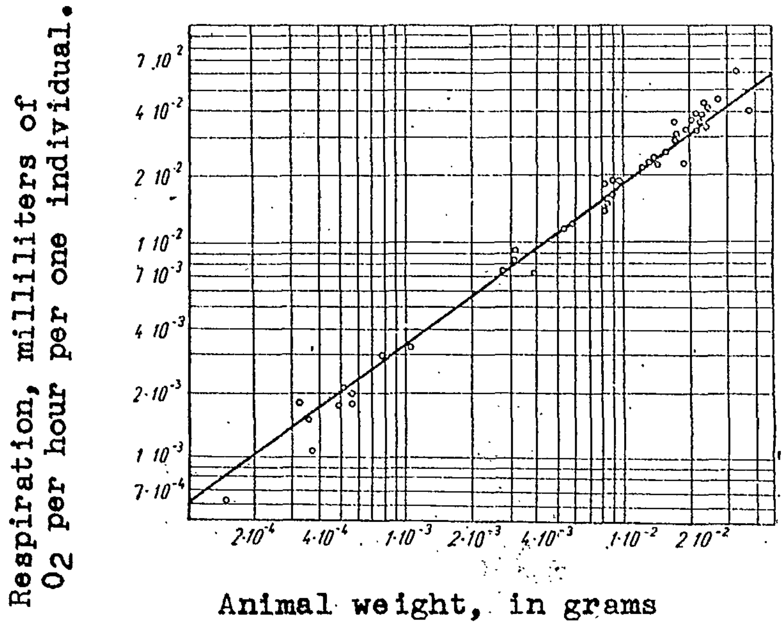

Figure 2. The respiration intensity of O. bottae in relation to the body weight.

No sexual differences were observed in the oxygen consumption, therefore, the observation results for males and for females are plotted on one and the same straight line.

As the animals in the respirometer were almost immobile during the experiment, the stated values of oxygen consumption should be considered as being close to the basic metabolism.

<u>Growth of orchestia</u>. Study of growth is very important in the determination of the energy balance in animals, insofar as the major part of the energy assimilated by the animals is spent on the growth processes.

We used two different methods of solving this problem.

First, we carried out experimental work on the determination of the animal growth. Two groups of crustaceans were used: recently born juveniles with an average initial weight of 0.340 milligram and animals with an initial weight of 29 milligrams. Between twenty and one hundred crustaceans of each group were kept in glass crystallizers on cystozirae from littoral refuse. In experiments with small animals, total weighing of the crustaceans was carried out every 10 days, while in experiments with larger crustaceans, this was done at longer intervals. By means of the total weight /60
and number of crustaceans in a sample the average weight of an individual was calculated. Thus, growth data were obtained for two groups of animals with different initial weight.

Secondly, growth curves were calculated from the metabolism level. G.G. Vinberg (see present compendium) proved recently that the metabolism and growth of animals are subject to a definite mathematical relation and that the growth curve may be calculated for a given temperature on the basis of respiration and other indices (coefficient of the energy utilization on growth of second order, K_2, initial and final weight of animals, calorific value).

If the animals of the given species reach the final (full-grown) size during the growth process, then the absolute weight increment (w) at a given time t is expressed by the following equation:

$$w_t = \left[W(1-\frac{a}{b}) - \left(W(1-\frac{a}{b}) - w_o(1-\frac{a}{b}) \right) e^{-(1-\frac{a}{b})kt} \right]^{\frac{b}{b-a}}, \quad (7)$$

where w_t is the determined value of the absolute increment, t is the time of growth (in days), W is the full-grown weight of the animal of the given species, w_o is the initial weight of the animals, e is the base of natural logarithms, a and b are constants indicating to what degree and how the growth of the given object differs from the growth with preservation of the geometrical shape.

The constant k depends on the interrelation of metabolism, weight and maximum value of K_2 of the given object and it may be expressed by means of the following equation:

$$k = \frac{T_1}{W^{(1-\frac{a}{b})}}\left[\frac{(K_2)_m}{1-(K_2)_m}\right] = \frac{T_1}{W^{(1-\frac{a}{b})} - w^{(1-\frac{a}{b})}}\left(\frac{K_2}{1 - K_2}\right), \quad (8)$$

where T_1 is the energy expenditure on metabolism per one unit of the animal's biomass. In other words, this value indicates the portion of the biomass of an animal with an individual weight of one unit (for example: one gram), which is spent in the metabolism process in one unit of time.

Table 3 shows results of orchestia weighings. The average weight increment for the given period is determined by means of three parallel experiments. We see from the table that this increment is almost identical in all three experiments. The growth increments were superimposed on several growth curves calculated according to respiration at 20°C with various initial values of K_2. It turned out that the results obtained in the experiments coincide well with the growth curve for which the maximum value K_2 is assumed to be 0.6 (Fig. 3). In numerical form the equation of the growth curve of the given instance is:

$$w_1 = \left[(0.576 - 0.45)\, e^{-0.0143\, t}\right]^4 . \quad (9)$$

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The following values and ratios were used for the derivation of this equation:

1) respiration in relation to the wet weight of the animals was determined by equation (6);

Table 3

Weight increment of orchestia (in milligrams) in relation to the growth, at a temperature of 20 ± 1.5°C.

Beginning of the experiment and the initial average weight of an animal	Number of crustaceans	days 10	20	30	40	50	60	120
19.VI 1965 г., 0,34 мг milligram	100	1,36	3,00	5,33	9,88	17,93	—	—
	100	1,23	3,07	4,34	9,69	13,06	—	—
	100	1,05	2,90	4,72	9,47	14,52	—	—
	Среднее Average	1,21	2,99	4,76	9,70	15,17	—	—
19.VI 1965 г., 0,74 мg	100	2,33	4,03	5,86	9,57	15,87	—	—
	100	2,90	5,86	7,72	11,30	15,98	—	—
	100	2,08	3,88	4,08	9,82	14,80	—	—
	Среднее Average	2,44	4,88	5,89	10,23	15,55	—	—
19.VI 1965 г., 29,0 мg	20	—	42,05	—	—	59,00	64,20	91,40
	50	—	41,20	—	—	56,60	64,75	90,20
	100	—	39,75	—	—	55,40	62,45	85,92
	Среднее Average	—	41,00	—	—	57,00	63,80	89,07

2) final (full-grown) weight (W) = 0.12 gram;

3) initial value $K_2 = 0.6$;

4) coefficient $v = \frac{K_2}{1 - K_2} = 1.5$;

5) calorific value of one gram wet weight of crustaceans is 1.5 kilocalories;

6) $\frac{a}{b} = 0.74$;

7) $W^{(1-\frac{a}{b})}$, or $W^{0.26} = 0.576$;

8) $\frac{b}{b - a} = 4$;

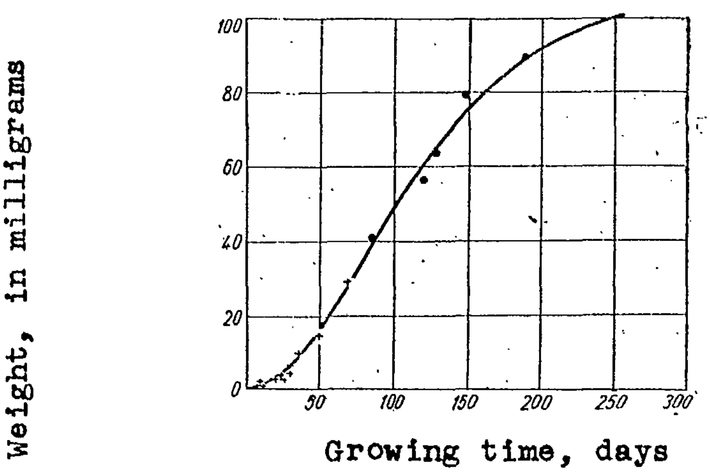

Figure 3. Weight increment curve for O. bottae when growing at a temperature of 20°C calculated according to equation (9); " + " is the absolute growth increment in experiments with newborn animals; " • " is the absolute growth increment in experiments with animals at an initial weight of 29 milligrams.

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9) $T_1 = 0.021$;

10) $N = T_1 \cdot v = 0.0315$;

11) $k = W^{-(1-\frac{a}{b})} \cdot N = 0.055$;

12) $e^{-(1-\frac{a}{b})\,kt} = e^{-0.143\,t}$;

13) initial weight of the animals (w_o) = $3.49 \cdot 10^{-4}$ grams;

14) $w_o^{(1-\frac{a}{b})}$, or $w_o^{0.26} = 0.126$.

Values of absolute increment of newborn animals, for which the beginning of the period is known (data of our experiments), were initially plotted upon the growth curve arrived at by calculation. They coincided well with the curve, therefore, we were also able to plot on this curve the results of experiments with larger animals, i.e., with the initial weight of 29 milligrams. The growth period of animals, prior to this weight, was determined by means of the theoretical curve.

As we see from the figure, the weight data coincide here equally well with the path of the curve. All this permits us to believe that the curve calculated for respiration reflects correctly the growth of orchestia, while the obtained equation of this curve, when appropriate temperature corrections are introduced for the respiration of animals, may be utilized for the determination of curves for individual growth of animals in various seasons of the year.

The increment of the animals may be evaluated not only by the above-mentioned methods, but also on the basis of the change in the size-composition of the population with time. From available field data from both bays the changes in the average weight of the animals were determined for their transition from one size-group to another. In Table 4 the data of field measurements are compared with the corresponding theoretical values obtained from the growth curve. The temperature of the refuse during the period of animal collection fluctuated between 18 and 28°C. Therefore, we have converted the initial values of increments calculated on the basis of these data to 20°C by means of coefficients from Krog's "normal curve". As we see from the table, in the majority of cases, particularly in the Golubaya Bay, the increment values determined according to the size-groups in the population were somewhat higher than those calculated by means of the growth curve, especially in young animals. For example, in the size-group 2 to 4 millimeters, this difference is maximal in the Golubaya Bay and constitutes 46% of the increment calculated by means of the curve. These

differences decrease with the age of the animals. A converse relation is observed in the size-group of 12 to 14 millimeters. Here, according to the field data, in the Golubaya Bay and in the Omega Bay, the increment was 44 and 18.5% lower respectively. Regardless of these differences, the increment values, obtained according /63
to the age composition of the animals, must be accepted as being very close to the theoretical ones of the growth curve. It should not be forgotten that the accuracy of such calculations is somewhat below the experimental determination of growth.

The fact that the growth increment of animals determined by means of 3 different methods (according to the field data, according to the curve calculated on the basis of respiration and coefficient K_2, and, finally, according to the dynamics of the size-composition of the population) is expressed by very similar values, we believe, is of exceptional interest. This is one more confirmation of the good prospects for determining the growth of the animal from its metabolism, as suggested by G.G. Vinberg.

Table 4

Values of daily increments calculated by means of the growth curve and field data.

Size-group, in millim.	Average Wet Weight, in milligrams	Daily increment (by growth curve)		Daily increment (by field data)			
				Golubaya Bay		Omega Bay	
		Milligrams	% of initial weight	Milligrams	% of initial weight	Milligrams	% of initial weight
1—2	0,600	0,080	22,9	0,062	19,7	0,050	14,3
2—4	1,700	0,137	22,8	0,200	33,3	0,169	28,2
4—6	5,18	0,248	14,6	0,192	11,3	0,168	9,9
6—8	11,43	0,398	7,7	0,475	9,2	0,485	9,4
8—10	21,08	0,536	4,7	0,755	6,6	0,515	4,5
10—12	34,78	0,652	3,1	1,010	4,8	1,010	4,8
12—14	53,20	0,682	2,0	0,383	1,1	0,556	1,6

Energy balance. The analysis of the energy balance of orchestia was carried out by means of the generally accepted method, which may be expressed by the equation suggested by G.G. Vinberg (1956):

$$P = \Pi + T + H,$$

where P is the energy quantity in the consumed food, which is measured by the sum of energy spent on growth (Π), respiration (T) and lost on isolation of non-assimilated food portion and of the metabolism products (H).

Another important eco-physiological aspect of the discussed problem is the determination of the efficiency of the utilization of assimilated energy on the growth processes of animals (Ivlev, 1939; Ivlev, Ivleva, 1948). We have already seen, that when calculating growth curves according to the metabolism level one has to operate with the coefficient of the utilization of the assimilated energy for growth (K_2). The value of this coefficient is determined by the ratio of the increment energy (Π) to the entire assimilated energy, i.e. to the growth increment energy plus the expenditure on the energy metabolism of the animal (T):

$$K_2 = \frac{\Pi}{\Pi + T} . \qquad (10)$$

This coefficient reflects the pure efficiency of growth in relation to the total value of assimilated energy.

Of considerable interest is also the coefficient of the utilization of the energy of first order (K_1) reflecting the gross efficiency of the growth. It is determined by the ratio of energy of the increment to the energy of the consumed food (P):

$$K_1 = \frac{\Pi}{P} . \qquad (11)$$

The basic elements of the energy balance were calculated on the basis of the above-mentioned energy balance for the orchestia with a wet weight of 9.2 to 78 milligrams (Table 5). The energy of consumed food (P) and the assimi- /65
lated portion of the energy are taken from experiments on alimentation (see Table 2); the respiration energy is determined by means of equation (6), where it was assumed that the consumption of one milliliter of oxygen is equivalent to liberation of 5 calories of energy; the value of the weight increment (Π) was determined according to the equation (9) and was converted to calories in accordance with data on the calorific value of animals. Comparison of the values of respiration and the increment values, expressed in calories, permitted us to calculate both coefficients of energy utilization for the growth of the animals on the basis of the

equations (10) and (11). We see from the stated figures that at obtained values of consumption and assimilation

Table 5

Daily (24 hours) energy balance.

Wet weight of one animal, milligrams	Daily ration	Assimilated food	Expenditures on respiration per 24 hrs.	Increment per 24 hrs.	Coefficient of energy utilization on growth of first order, K_1	Coefficient of energy utilization on growth of second order, K_2	$v = \frac{K_2}{1 - K_2}$
9,2	3,75	2,08	0,91	1,17	31,2	56,4	1,52
10,5	6,32	2,61	1,00	1,61	25,4	61,7	1,61
11,4	6,48	2,82	1,06	1,76	27,1	62,4	1,66
12,4	5,47	2,46	1,13	1,33	24,3	64,0	1,17
14,1	5,92	2,42	1,25	1,17	19,7	48,2	0,94
15,2	5,60	2,31	1,32	1,00	17,9	43,4	0,76
20,0	7,45	3,00	1,62	1,48	19,9	49,4	0,98
25,4	10,60	3,39	1,93	1,46	13,8	43,0	0,75
34,4	10,10	3,74	2,42	1,32	13,1	35,3	0,55
35,7	11,50	4,09	2,48	1,61	14,0	39,2	0,65
45,0	13,90	4,74	2,94	1,80	13,0	38,0	0,61
65,0	16,00	4,88	3,42	1,46	10,1	30,0	0,43
60,0	17,40	5,96	3,65	2,31	13,3	38,8	0,63
61,7	19,00	6,10	3,71	2,39	12,6	39,1	0,64
63,0	17,70	5,95	3,77	2,18	12,3	36,5	0,58
68,0	14,30	5,94	3,98	1,96	13,7	33,0	0,50
70,7	17,30	6,15	4,10	2,05	11,8	33,4	0,50
76,6	19,20	6,06	4,36	1,70	8,9	28,0	0,39
77,9	19,80	6,02	4,42	1,60	8,1	26,5	0,36

the growth increment energy is 8.1 to 31.2% of the energy in the consumed food (K_1) and 26.5 to 62.4% of the energy in the assimilated food (K_2). The highest values for both coefficients are obtained in young animals. Their energy portion, spent on body mass increment, is equal to or exceeds the energy spent on the energy metabolism of the organism. This relation becomes reversed with the increase in weight and, consequently, also with the increase in the animal's age, the respiration energy begins to a considerable degree to prevail over the growth increment energy. Values of the coefficients K_1 and K_2 decrease correspondingly.

It was shown previously that there is a definite quantitative relation between the growth and the respiration. One may say, on the basis of the foregoing , that the growth increment of the organism equals its respiration (T) multiplied by a certain coefficient v:

$$\Pi = vT. \qquad (12)$$

This coefficient is greater than one, when the growth increment energy exceeds the respiration energy, and it is less than one when the relation is reversed (Table 5). In other words, it is determined by the maximum value of K_2. Mathematically the relation between v and K_2 may be expressed in the following manner:

$$v = \frac{K_2}{1 - K_2} . \qquad (13)$$

With the attenuation of growth of the animals, the value v correspondingly decreases along with decrease in the value of the coefficient K_2.

Discussion of the Results.

The foregoing data permit us to note certain characteristic peculiarities in the changes of the main elements in the energy balance during the growth process of the orchestia.

The absolute dimensions of the rations increase regularly with the increase in the individual weight of an animal, but their relative value in percentage of the body weight decreases. To a certain degree the value of the assimilated portion of the food also decreases in relation to the ration (from 50 to 30%. In general, the degree of assimilation of food by orchestia should be considered low. Probably, this is connected with peculiarities of the food, which consists to a considerable degree of components that are hard /66 to digest, or which are highly decayed and of a material devaluated in food value.

We also observe an inverse relation between the energy spent on respiration and energy spent on the animal's growth. As we see from Fig. 3, the growth curve of the orchestia has an S-shaped character indicating that the growth rate of the animals, after a certain size is reached, decelerates noticeably and approaches zero. Correspondingly, there is also a decrease in the portion of energy spent on the increment in the body mass of the crustacean, i.e. on the plastic metabolism. In the meantime, expenditures on energy metabolism continue to increase, insofar as the absolute weight of the animals increases.

Of indisputable interest is the analysis of the coefficients of energy utilization on growth. The value K_1 is often called "growth efficiency" in the literature, in other words one thinks about the gross efficiency of the growth (Makfed'en[1], 1965). According to Slobodkin (1960), this value in various animals and under various ecological conditions fluctuates between 6 and 37%. Our results (8.1 to 31.2%) virtually coincide with these data. However, we see from a number of studies on aquatic crustaceans, that the fluctuation range of these values may be still wider, namely:

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[1] Macfadden (McFadden)?? - Revisor.

from 4 to 50% (Richman, 1958; Lasker, 1960; Corner, 1961; Sushchenya, 1962, 1963, 1964). Undoubtedly, parallel to the specific peculiarities of the utilization of ènergy on growth in animals of various ages, certain external factors may also have effect upon this index; for example, excessive consumption of food when abundant in the medium, or an increase in the energy consumption on the search for food, when food is scarce. There may be a considerable number of biological situations leading to an increase in the energy metabolism and to a corresponding decrease in the proportion of energy used on the increment of the body mass.

Makfed'en (1956) points out that the growth efficiency in domestic animals, as understood in the above sense, fluctuates within the range of 5 to 50%, depending on the age. For terrestrial invertebrates the average value quoted is approximately 15% (Gere, 1957). As we see, all these data coincide sufficiently well and trace the limits of the changes of the gross efficiency of the growth in all the animals in general.

When the given value is determined for large animals, consideration is often given to not only the energy which is spent on the process of individual growth of the animal, but also the energy spent on its parturition. In our case, the latter value is very small compared to the total energy spent during the life of the given individual. When newborn crustaceans weigh 0.349 milligram, the energy /67 contained in the tissue of their body is only about 0.5 calorie. We therefore disregarded this value.

The initial value K_2, in accordance with the growth curve in the given species of orchestia, is 0.6. This value differs somewhat from the K_2 value shown in Table 5, where a similar level of the given coefficient is obtained in animals weighing from 9.2 to 12.4 milligrams. The reason for this discrepancy, we believe, is hidden in the fact that, in the balance table, the energy expenditures on respiration calculated by means of equation (6), which practically reflects the basic metabolism, are somewhat lower than the values of the true metabolism in animals in the experiments on the study of alimentation. It has been visually noted that in cages, during the study of alimentation, the animals were more active than in the respirometers, and, consequently, were expending more energy on respiration. Thus, the energy expenditure on active metabolism of the animals, not taken into account here, leads to excessive values of increments shown in Table 5.

The correct determination of the K_2 value achieves special importance, because of the present possibility of strictly mathematically relating the metabolism level in animals to their growth rate. Inaccuracies in the determination of the assimilated energy or of the respiration intensity, which occur to greater or lesser degrees during the setting-up of experiments, can noticeably distort the true value of K_2.

It is important to have an accurate value of this coefficient for at least one of the weight-groups of the given species. It is naturally preferable to know its initial (maximum) value, since it is this value that is directly applied in the equation of the growth curve. However, when working with larval stages of many invertebrates it is often methodologically difficult to achieve the above value. The determination of K_2 may be more successful in the older age-groups. In such cases, by using the coefficient v, one can establish the maximum value of K_2 characteristic of the two first stages of growth. It is indicated above that v is connected with K_2 by a simple relation (13). On the other hand, K_2 is a function of weight:

$$\frac{K_2}{1 - K_2} = f(w).$$

Consequently, knowing K_2 for animals of a given weight w, it is easy to determine the corresponding value of v. The value of the latter may be also expressed by another equation:

$$v = v_o \left[\frac{W^{(1-\frac{a}{b})} - w^{(1-\frac{a}{b})}}{W^{(1-\frac{a}{b})}} \right], \qquad (14)$$

from here:

$$v_o = \frac{v}{\left[\frac{W^{(1-\frac{a}{b})} - w^{(1-\frac{a}{b})}}{W^{(1-\frac{a}{b})}} \right]} \qquad (15)$$ /68

where v_o is the initial value of the coefficient v for the juveniles of the given species, w is the weight of animals at a value v established by us, and W is the full-grown (final) weight of an animal of the given species. The value of the constants a and b was explained previously.

With the initial value $v = v_o$, we determine the sought value of K_2 by means of consecutive substitution of various K_2 values into the equation (13).

Thus, for example, knowing that an animal weighing 53.2 milligrams, or 0.0532 gram has a v value of 0.31, and the full-grown weight of an animal of this species is 0.12 gram, we find by means of equation (15) that $v_o = 1.5$. To this value corresponds $K_2 = 0.6$:

$$v_o = \frac{0.6}{1 - 0.6} = 1.5.$$

This method will, to a certain degree, facilitate the determination of the growth curve according to the intensity of metabolism, as well as the determination of the corresponding energy expenditure on the plastic metabolism in invertebrates with small juvenal stages. However, calculation by means of K_2 should be considered exclusively as a special case. The method of direct determination of the animal's growth should be considered as the basic method.

CONCLUSIONS.

1. It is established that the weight of *Orchestia bottae* (W) is connected to the body length (l) by a relation raised to a power close to three. The equation of the above relation is the following:

$$W = 0.121\, l^{2.75}.$$

2. The water content in the orchestia body is a constant value. The dry weight of the crustaceans (W_1), regardless of their age, is on an average 32.4% of the wet weight (W). The relation between these values may be expressed by the most simple equation:

$$W = 3.09\, W_1 .$$

3. The average annual calorific value of the population constitutes 4.7 kilocalories per one gram dry weight, the ash-content constitutes 20% of the dry weight. The calorific value of food in decaying refuse of cystozira is 1.2 kilocalories per one gram of wet weight, the average calorific value of the feces excreted by orchestia is 0.834 kilocalories per one gram of wet weight.

4. The ration of the animals in the 24-hour experiments /69
fluctuated between 48.4 and 77.3% of the body weight, the

average degree of assimilation is 40.2%. In the short-term experiments, converted to 24-hour periods, the size of the ration is from 17.5 to 50% of the body weight, the average degree of assimilation is 35.4%.

5. Respiration of orchestia (Q) is subject to ordinary parabolic dependence from the body weight (W), and converted to wet weight of one single animal it follows the equation $Q = 0.243 W^{0.74}$ (milliliters of O_2 per hour per one single animal).

6. The growth curve of the given species is S-shaped. At a temperature of 20°C, the females attain sexual maturity in 2-2.5 months. The wet weight of an individual female, at that time, is 30 to 40 milligrams. The maximum recorded weight of the animals is 120 milligrams; it is attained by males exclusively. It has been proven possible to calculate the growth curve of <u>O. bottae</u> from the metabolism level. A numerical expression of the corresponding equation is shown.

7. In young animals approximately 30% of the energy of the consumed food and approximately 60% of the assimilated energy are utilized on growth. In animals of the older age-groups these figures are 10% and 30% respectively.

8. In animals weighing between 9 and 78 milligrams, the energy expenditure on respiration, in relation to the assimilated energy, is increased from 43.8 to 73.4%.

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THE ELEMENTS OF ENERGY BALANCE OF *ORCHESTIA BOTTAE* M.-EDW. (AMPHIPODA—TALITROIDEA)

L. M. SUSHCHENYA

Summary

The article deals with the investigations of some parameters in determining the quantitative contribution of *O. bottae* to energy turnover at inshore zone of the Black Sea. This species was studied at different stages of its life from July 1962 to June 1963. The received data show that the mean value of food consumption (R) ranged from 17.5 to 77.3% of body weight per day. The efficiency of assimilation (a) during feeding with dead *Cystoseira* were in the range from 31 to 51%. The relation between the weight of *Orchestia* (W) and its rate of oxygen consumption (Q) at 20° C is expressed by equation $Q=0{,}243\ W^{0{,}74}$. The energy utilized for growth (G) was estimated by the growth curve received empirically and calculated at the same time on the level of respiration. The growth was converted to units of energy according to caloricity of *Orchestia* (4,7 Kcal/g). It shows that the gross efficiency of growth ($\frac{G}{R}$) *Orchestia* ranging in weight from 9 to 80 mg decreased in average from 30 to 8%, the net efficiency of growth ($\frac{G}{aR}$) from 60 to 30%.