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Nutrition and energy balance of tropical copepods (136)*

by T.S. Petipa, A.V. Monakov, A.P. Pavlyutin, Yu.I. Sorokin

The quantitative evaluation of concrete productive capacities of any community of organisms or its separate links depends on the rate of energy ingestion and the further use of this energy in the food webs of the community. In order to establish the nature of the distribution and utilization of energy within the community, it is necessary to study the matter and energy balance of its main ecological groups. This was undertaken in 1971 during an expedition to the tropical zone of the Pacific Ocean on board the research vessel "Vityaz". The expedition was organized by the Institute of Oceanology of the USSR Academy of Sciences and was devoted to studying the productivity of tropical pelagic communities (50th expedition).

The main task of this undertaking was to determine all the elements of food balance in tropical copepods from a typical ocean community having a stable structure with maximum approximation to natural conditions. Small crustaceans belonging to different ecological groups were the subject of study.

*The numbers in the right-hand margin are the pages of the Russian text - translator

Method

The energy balance of tropical copepods was studied using the radiocarbon method developed by Yu.I. Sorokin (1966), which was described in greater detail by Petipa, Pavlova and Sorokin in its application to marine organisms (1971).

In stable ocean waters we observe a well-defined stratification in the distribution of all forms of suspended organic matter. In this case we usually observe large accumulations of dead and living organic matter at the boundaries of abrupt change in medium factors (thermocline and halocline, sudden decrease in the amount of light, diminution of biogens, etc.). Maximum accumulations of organic matter were registered in the thin water layers of the relatively stable waters of the tropical zone of the Pacific (Vinogradov, Gitel'zon, Sorokin, 1971) (fig. 1). These layers abound in numerous minute and large vagile animals which are apparently capable of assimilating the highly accessible and diverse food there.

Taking into account the established peculiarities in the distribution of organisms, the experiments on the food balance of copepods were carried out with a mixture of bacteria, algae and animal organisms. The ratio of the food groups and their concentration corresponded with those observed in the layer of maximum accumulation of organic matter, the overall concentration of the food organisms amounting to 1500-3000 cal/m^3 or 1-3 g/m^3. (137)

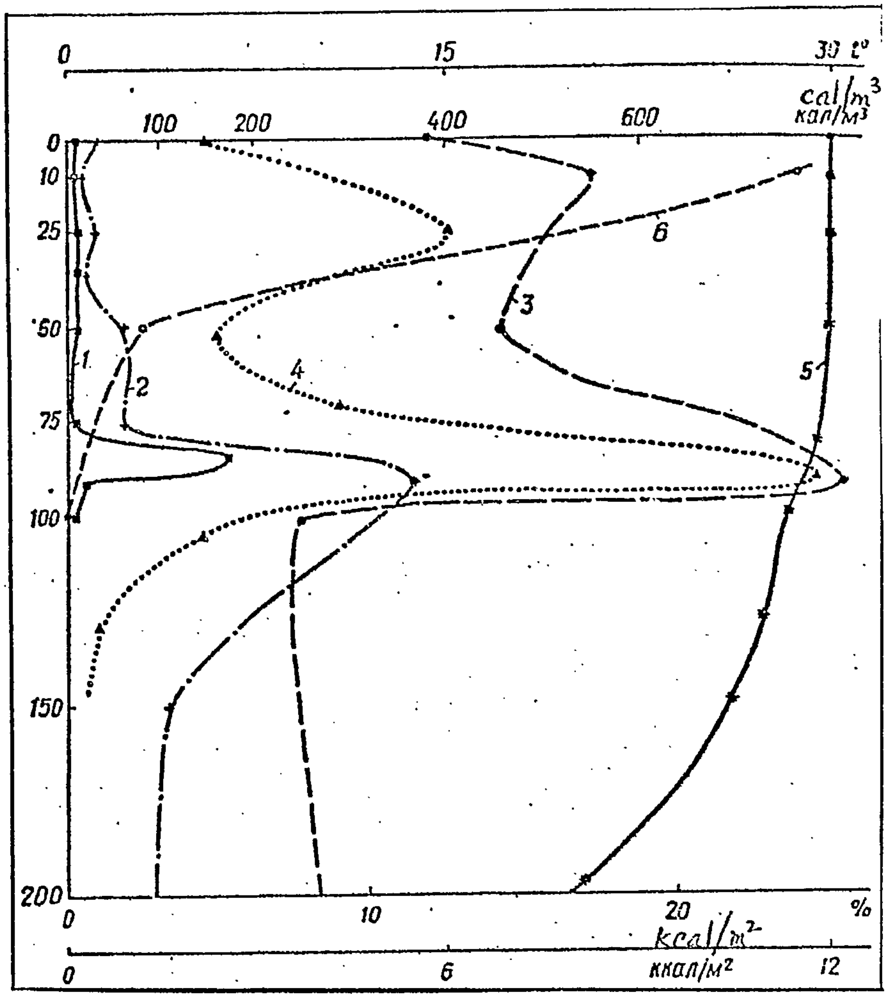


Fig. 1. The approximate vertical distribution (in cal/m^3) of bacteria (1), phytoplankton (2) and organic suspension (3), and the intensity of bioluminescence (4, %), temperature (5, °C) and the intensity of light (kcal/m^2) in stable tropical waters of the Pacific Ocean. The graph is based on materials of the 44th expedition of the "Vityaz" research vessel.

The daily food balance was expressed by the equation

$$R = C_d + R_c + R_s + R_d,$$

where R stands for ration, C_d - the amount of matter or energy accumulated in the body, R_c - the loss of labelled food during respiration, R_s - solid excreta (feces) and R_d - liquid organic excreta; $C_d + R_c = U$ (assimilated food), $R_s + R_d = F$ (unassimilated food); $\frac{U}{R}$ expresses assimilability. Each determination of the components of the food (138)
balance in this or that crustacean included three experiments, which corresponds to the number of food types. Each type of food was in turn labelled with C^{14}. The full daily ration was determined by totalling the corresponding labelled components of balance obtained for the three types of food. The daily rhythm of feeding was taken into account when evaluating daily rations and other component parts of the food balance, and so observations were conducted both during the daytime and at night. The time during which the animals were fed on labelled foods corresponded with the time required for digestion.

Simultaneously with the basic experiments, we tested various techniques for producing more accurate readings of the amount of feces excreted by the animals and the amount of carbon dioxide respired by them, after which corrections were introduced. The accuracy of the animal rations was verified by comparing the amount of food assimilated by them with their food requirements calculated on the basis of energy utilization. The latter was determined by the amount of oxygen taken up by the crustaceans in fairly large closed tanks using Winkler's method (Shushkina, Pavlova, 1973).

In the balance experiments we used cultures of bacteria, algae and animal organisms obtained by L.A. Lanskaya, primarily from various depths of the study area in the Pacific. The most frequent food items consumed were Amphidinium klebsi of the small algae, Streptotheca thamensis of the large algae, natural bacterioplankton, and a mixture of small calanids Undinula darwini, Eucalanus attenuatus, Temora stylifera, Paracalanus parvus and Scolecithrix danae. All the parameters of the balance experiments were expressed in absolute and relative values - in calories and percentage of the weight of the organism expressed in energy units. The amount of carbon in the animal bodies was determined using two methods - the method of wet combustion with titration of the bichromate spent on the oxidation of the organic matter, and the direct method consisting in combustion in a chromium sulfate mixture with subsequent determination of the evolved CO_2 in an automatic recording coulomb-meter (Lyutsarev, 1968). Both methods produced similar results.

A total of 154 experiments with 14 species of animals was devoted to studying the elements of energy balance; 8 of these experiments were concerned with the improvement of methods.

Results

The most complete and detailed study of the components of the balance equation was made with six species of tropical copepods belonging to a number of ecological groups. These included the following:

Undinula darwini - a weakly migrating species ($2 - 2\frac{1}{2}$ mm)
inhabiting the upper 50-100 m layer, primarily a plant-eating form (139)
according to a number of authors;

Pleuromamma abdominalis - a large (4-4½ mm) crustacean which migrates intensively within the 50-500 m range, known to forage on mixed food of plant and animal origin;

Candacia aethiopica and *Euchaeta marina* - weakly migrating copepods of the upper 200-300 m layer, average size 2.2 - 3 mm, considered by most authors to be typical carnivores.

Oncaea venusta - non-migrating species of the so-called suctorial carnivores; primarily inhabits the upper layers of the sea (up to 250 m); small form up to 1.2 mm in size.

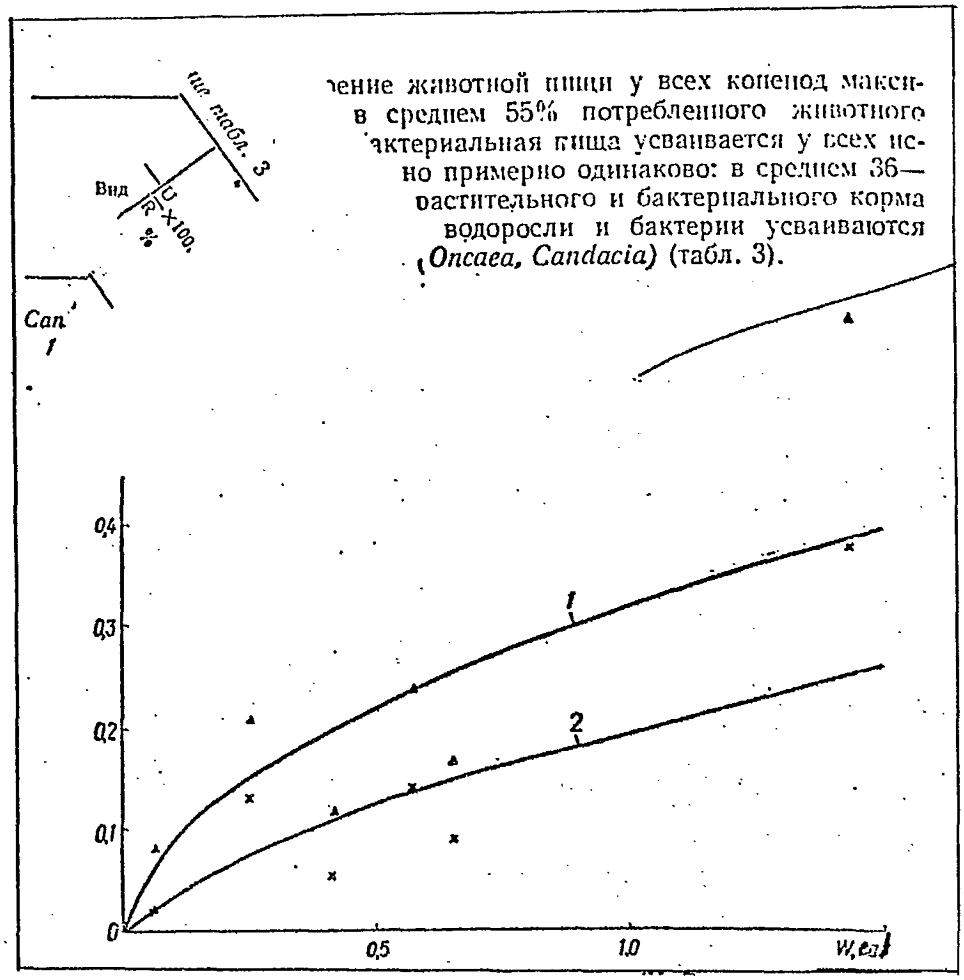
Rhincalanus nasutus and *R. cornutus* - slow-moving, hovering yet migrating inhabitants of the deeper layers (from 100-200 to 500 m); size 3-3½ mm; known to be plant-eaters.

The results of direct determinations of the initial components of the balance equation derived in brief experiments ($R_1 = R_2 + r_c + r_s + r_d$) with the indicated species are given in table 1, the results of the calculations of daily balance indices ($R = C_d + R_c + R_s + R_d$) in table 2, and the composition of the daily ration in table 3. The data in table 3 indicate that when maintained on mixed food, the studied species of tropical copepods (from 1 to 4½ mm in size) consumed all the groups of food - bacteria, algae and animal organisms. However, the degree of uptake of this or that food by copepods varied. The uptake of animal food was at its maximum in all the copepods (51-92% of the ration). Bacterial food comprised the smallest portion (1.3-4%) of the ration of the carnivorous *Euchaeta*, *Candacia* and *Oncaea*. Bacteria constituted 8-14% of the ration of *Undinula*, *Rhincalanus* and *Pleuromamma*. The relatively small algae (Amphidinium and others) used in the experiments were consumed to the highest degree (up to 35%) by the species (Undinula) capable of directing their food to the mouth by rotating their oral extremities over a lengthy period of time. For the other species, including the basically carnivorous ones, small algae comprised 6-22% of the ration.

Special experiments were conducted to evaluate the consumption of large algae by crustaceans. It was found that many of the species consumed considerably greater amounts of large algae (Streptotheca thamensis) from the mixture of food than they did small algae (table 4). The role of large algae in the ration of the large consumers of mixed food (Pleuromamma) and certain carnivores (Candacia) increased quite abruptly (by 10-15 times). At the same time, the large and small algae were found to be of almost equal importance in the ration of the other predacious forms (Euchaeta, Oncaea) (table 3 and 4).***

Overall average daily assimilability ($\frac{U}{R}$) in tropical copepods during mixed feeding fluctuates from 30 to 64%, an average of 52%. The lowest degree of assimilability (30%) was observed in small Oncaea (table 2). A comparison of assimilability values during the daytime and at night for all the copepods revealed a definite tendency, this being that at night assimilability in predacious crustaceans (Euchaeta, Candacia and Oncaea) was twice higher than during the daytime, and almost the same in copepods feeding on mixed nutrients (in our case Undinula, Pleuromamma, Rhincalanus) (table 2).

***The remainder of the paragraph is untranslatable due to careless xeroxing of the original text - translator



(146)

Fig. 2. The dependence of the consumption (R, 1) and assimilation (U, 2) of food on body weight in tropical copepods at 27-29°C.

$R = 0.318W^{0.523}$.

Deviation of measurements relative to the theoretical curve is equal to ± 0.186.

$U = 0.196W^{0.738}$.

Deviation of measurements relative to the theoretical curve is equal to ± 0.233.

Unassimilated substance (F), consisting of solid and liquid excreta, comprised 36-70% of the ration or 13-89% of the body weight in the studied species when mixed food was consumed. The solid excreta R_s (feces) in all the copepods comprised 5-51% of the weight of the crustaceans. In Pleuromamma, Undinula and Rhincalanus the amount of solid excreta was 2-3 times greater than that of liquid excreta with even a small difference in the consumption of plant and animal food. In these species, solid excreta comprised 10-24% of the body weight, the liquid excreta 3-8%. With basically predacious foraging, either the reverse was observed or the amounts of solid (5.5-51%) and liquid (7-37% of the body weight) excreta were equal (table 2). (147)

The full daily ration in the discussed species (1 to 4½ mm in size, energy content from 0.065 to 1.4 cal/specimen) fluctuated from 27 to 127% of the body weight (table 2). The relative ration diminished as the size and weight of the crustaceans increased. The dependence of the daily ration of the studied tropical copepods on the weight of their body, expressed in energy units (fig. 2) can be described by the following formula:

$$R = 0.318W^{0.523}.$$

The dependence of the amount of food assimilated over a period of 24 hours on the body weight of the crustaceans, expressed in energy units, was found to be similar - $U = 0.196W^{0.798}$.

The diurnal rhythm in the feeding of tropical copepods in brief experiments shortly after the crustaceans had been caught was clearly defined. In the forms inhabiting the upper layers down to

150 m (Undinula, Candacia), nighttime foraging was twice as intensive as daytime feeding; in copepods descending to depths of 300 m (Oncaea, Euchaeta) it was four times more intensive; and in crustaceans inhabiting the 300-500 m layer during the day (Pleuromamma, Rhincalanus), nighttime foraging was ten times more intensive than daytime feeding (table 2).

The data obtained on the food balance of tropical copepods were used to determine the feeding selectivity of the studied species. Selectivity was judged on the basis of the electivity index ($E = \frac{A_n - A_c}{A_n + A_c}$ introduced by V.S. Ivlev (1955). A comparison of the electivity indices of different copepod species has enabled us to draw the following conclusion.

Undinula and Rhincalanus are capable of actively selecting animal organisms, algae or bacteria depending on the size ratio of the food items and their concentration in the medium. Pleuromamma and Candacia actively select animals and algae, especially those of a large size. Euchaeta selects animal organisms and sometimes algae, usually avoiding bacteria. Oncaea is capable of actively selecting small and large animal organisms and algae, actively avoiding bacteria (table 5). (149)

Discussion and Conclusions

The present study is a continuation of the investigations on the feeding of tropical zooplankton, conducted during the 44th expedition of the "Vityaz" research vessel to the tropical zone of the Pacific in 1968-1969.

During this voyage, a study was made of the food composition of the most prolific tropical copepods belonging to different ecological groups, and a dependence established between the consumption and utilization of the different types of food and their concentration. The crustaceans were maintained on monocultures of various food items. It was found that copepods in the tropical zone possessed a high degree of trophic plasticity and were capable of consuming the most diverse food organisms. However, a comparison of the determined ration of the copepods (mainly its assimilated portion) with their theoretical food requirements showed that the food requirements of the crustaceans were not satisfied by any one type of food, be it algae or bacteria. Only food of animal origin supplied the copepods with a balanced ration. The results of this work have permitted us to assume that most of the copepod species must be omnivorous in stable tropical waters with a low biomass of plankton and other suspended organic matter and a great diversity of species, and that the degree of predaciousness of the planktonic animals sharply increases (Petipa, Pavlova, Sorokin, 1971).

In order to solve this question once and for all, it was necessary to study the food balance of the copepods as they foraged on mixed foods, which could be observed in natural conditions at sea. We therefore undertook a new approach by applying the radiocarbon method to evaluate the degree of consumption and assimilation of various organisms (animal, algae, bacteria) from a mixture of these foods by marine copepods.

The obtained results fully substantiated the assumptions made earlier. Indeed, in stable waters where there is no constant and strong enough influx of biogens or any development of a high biomass of initial producers, most of the zooplankton (copepods) are omnivores with the consumption and assimilation of animal foods at a maximum level in all the species. Only when mixed foods are consumed do the tropical copepods satisfy their respiratory needs (see table 2).

An analysis of the acquired data showed that in tropical stable waters the zooplankton should not be divided into carnivores, plant-eaters and omnivores. The particular ratio of food organisms in the ration of copepods probably depends on the peculiarities of the functional morphology of their mouth parts, certain physiological properties and the distinctive conditions of their habitat. All these factors characterize the feeding type of the animal. We therefore believe that it would be more correct to divide the organisms with respect to all their potential (150)
capacities and the distinctive conditions of their habitat in order to properly evaluate their role in the food webs of the communities. New types of copepod nutrition will be discussed in a separate paper.

Having analyzed the particular results of the present study, we can say that the dependences of the daily ration of tropical copepods and its assimilated portion on body weight at 27-29°C are expressed by equations similar to the ones derived for copepods and other crustaceans from temperate waters at 17-25°C, the exponents of weight (W) in the formulas for tropical copepods not exceeding the standard values of this coefficient (Sushchenya, Khmeleva, 1967; Sushchenya, 1969; Petipa, 1971).

Experiments have shown that when copepods feed on a mixture of different food organisms contained in the medium in an excessive amount (a phenomenon observed in the thin water layers mentioned earlier), the crustaceans mostly select and consume any type of food which is the most accessible and satisfying to them. These foods are usually animal organisms and large algae for the relatively large consumers (over 1.5 mm) and smaller animals and algae for the small ones (up to 1.5 mm). Bacteria on the whole play an insignificant role in the feeding of copepods (see tables 2 and 5).

The average assimilability of food (52%) during excessive mixed feeding is relatively low and differs insignificantly from the assimilability observed in experiments with one type of food also in an excessive amount (Petipa, Pavlova, Sorokin, 1971). As a rule, the foods which serve as "second choice" for the given species in the given conditions are the most poorly assimilated foods of all those available (table 3). The assimilability of certain types of food (e.g. algae) can deteriorate somewhat due to a large amount of poorly assimilable ash contained in them (Conover, 1966). On the other hand, the constant predators (Euchaeta and others) are apparently less adapted for digestion of plant foods. The high content of ash in plant foods is apparently why solid feces are far more profuse than unassimilated liquid excreta in copepods which feed largely or solely on algae (Petipa et al., 1971); the amounts of solid and liquid excreta are usually equal when the crustaceans forage mainly on animal foods (table 2, 3).

It is difficult to explain why assimilability diminishes during the daytime in forms that forage almost constantly on animal foods. Neither the composition of their food, their motor activity nor feeding intensity is likely to have any essential effect on this. It is therefore possible that the assimilation of food as a physiologi- (151)
cal process has its own particular and independent diurnal rhythm in carnivores.

The relatively low assimilability on the whole which is observed during excessive feeding is apparently due to the rapid flow of food through the intestine with rapid assimilation of the readily assimilable portions of it (e.g. liquid fats - oils). Such a means of utilizing and assimilating food is apparently more expedient, as it allows the animals to satisfy their food requirements more fully and quickly. The capacity to assimilate liquid fats quickly has already been analyzed (Petipa, 1964).

The previously noted regular change in the diurnal rhythm of feeding in experimental copepods inhabiting different water layers is apparently associated with the varying amplitude and intensity of their diel vertical migrations, or with the different degrees of motor activity during the daytime and at night. The crustaceans compensate for the energy spent on moving about by more intensive feeding at night. According to M.E. Vinogradov (1968), it is the Pleuromamma that in the tropics belongs to the interzonal intensively migrating species. A similar dependence has been established for the Black Sea (Petipa, 1964).

By comparing and critically analyzing the data available on copepod feeding (Mullin, 1966; Arashkevich, 1969; Samyshev, 1970; Vyshkvartseva, 1972, and others) we can make the following conclusion.

Copepods are capable of using various means of seizing their food and consuming a diversity of it in various environmental conditions due to the peculiarities of the functional morphology of their mouth parts and the physiology of their digestion. Depending on the particular conditions of the habitat, the copepods show preference for this or that type of food, which may alter as conditions change. At the same time, the formation of the feeding habits of copepods is influenced by the degree of their adjustment to certain food organisms. Thus, most copepods in the stable ocean waters in the tropical zone of the Pacific are consumers of the most diverse foods due to the specific environmental conditions (see above), the high-calorie foods of animal origin being the most important in their ration. Of lesser importance are plant organisms and bacteria. The consumption of mixed food by organisms living in tropical waters is also substantiated by the absence of strong differences in the respiratory level of tropical animals belonging to different ecological groups (Shushkina, Vilenkin, 1971).

References

1. Arashkevich E.G. The nature of copepod feeding in the northwestern part of the Pacific Ocean. Okeanologiya, 1969, 9, 5.

2. Vinogradov M.E. Vertical distribution of ocean zooplankton. "Nauka", Moscow, 1968.

3. Vinogradov M.E., Gitel'zon I.I., Sorokin Yu.I. The spatial structure of communities of the euphotic zone in tropical ocean waters. In: Funktsionirovaniye pelagicheskikh soobshchestv tropicheskikh rayonov okeana (Functioning of pelagic communities in tropical areas of the ocean). "Nauka", Moscow, 1971.

4. Vyshkvartsev N.V. The functional morphology of the mouth extremities and the phylogenetic relations of *Calanus* species (Copepoda, Calanoida). Author's abstract of Candidate's dissertation. Leningrad, 1972.

5. Ivlev V.S. Experimental fish ecology. Pishchepromizdat, Moscow, 1955.

6. Lyutsarev S.V. The method and apparatus for determining the amount of organic carbon in seawater. In: Metody rybo-khozaistvennykh khimiko-okeanograficheskikh issledovaniy (Methods of fishery and chemico-oceanographic investigations). Part II, ONGI VNIRO, Moscow, 1968.

7. Petipa T.S. The daily feeding rhythm and daily rations of Calanus helgolandicus (Claus) in the Black Sea Trudy Sevastop. biol. st., 1964, 15.

8. Petipa T.S. The feeding of planktonic organisms and their food interrelationships. In: Problemy morskoi biologii (Problems of marine biology). "Naukova Dumka", Kiev, 1971.

9. Petipa T.S., Pavlova Ye.V., Sorokin Yu.I. A study on the feeding habits of prolific plankton forms in the tropical zone of the Pacific Ocean by means of the radiocarbon method. In: Funktsionirovaniye pelagicheskikh soobshchestv tropicheskikh rayonakh okeana. "Nauka", Moscow, 1971.

10. Samyshev E.Z. Trophological and biochemical aspects of studying the components of seston in the tropical zone of the eastern Atlantic. Author's abstract of Candidate's dissertation. Sevastopol, 1970.

11. Sorokin Yu.I. The application of radioactive carbon for studying the feeding habits and food relationships of aquatic animals of inland waters. In: Trudy Instituta biol. vnutrennikh vod AN SSSR, 1966, 12, (15).

12. Sushchenya L.M., Khmeleva N.N. The consumption of food as a function of body weight in crustaceans. DAN SSSR, 1967, 176, 6.

13. Sushchenya L.M. The quantitative patterns of metabolism and the transformation of matter and energy by crustaceans. Author's abstract of Doctor's dissertation. Moscow, 1969.

14. Shushkina E.A., Pavlova Ye.V. The respiration rate and production of zooplankton in the equatorial part of the Pacific. Okeanologiya, 1973.

15. Shushkina E.A., Vilenkin B.Ya. The respiration of planktonic crustaceans in the tropical zone of the Pacific Ocean. In: Funktsionirovaniye pelagicheskikh soobshchestv v tropicheskikh rayonakh okeana. "Nauka", Moscow, 1971.

16. Conover R.J. Factors affecting the assimilation of organic matter by zooplankton and the question of superfluous feeding. - Limnol. and Oceanogr., 1966, II.

17. Mullin M.M. Selective feeding by Calanoid Copepods from the Indian ocean. - In: Some contemporary studies in marine science. H. Barnes (Ed.) London, Allen a. Unwin, 1966.

Table 1

The initial components of energy balance (substance accumulated in the body - R_2, secreted carbon dioxide - r_c, feces - r_s, excreted organic substance - r_d, ration - R_1) in tropical copepods as observed in a brief experiment at t = 27-27.5°C (cal x 10^{-4})

Species	Time of day	No. of experiments	No. of animals in experiment	R_2	r_c	r_s	r_d	R_1
Feeding on nutrients of animal origin (duration of experiment - 3 hours during the day and 1½ hours at night)								
Undinula darwini	daytime	3	10	30,91±18,97	28,90±14,72	27,27±11,79	13,46± 2,14	100,44±55,38
	nighttime	3	14	23,48± 5,63	33,97±19,32	22,37± 5,48	8,50± 2,75	88.32±41,63
Pleuromamma abdominalis	daytime	3	8	12,02± 3,96	96,59±30,55	5,04± 2,74	13,30± 6,68	126,95±34,91
	nighttime	3	6	11,25± 6,43	362,20±176,10	156,13±42,03	77,27±42.03	606,85±254.30
Candacia aethiopica	daytime	5	10	9,34± 4,41	7,53± 4,90	10,74± 6,66	50,30±22,61	77,91±49,59
	nighttime	4	12	6,50± 2,91	55,70±30,41	13,89± 5,36	27,90±18,24	104,00±39,68
Euchaeta marina	daytime	6	10	23,61±12,82	5,28± 0,53	8,30± 4,88	58,06±45,65	95,26±60,27
	nighttime	5	10	74,68±33,97	93,04±20,25	50,80±10,37	21,65± 7,62	240,12±34,84
Oncaea sp.	daytime	2	3	0,72± 0,42	4,00± 0,69	3,51± 1,36	3,86± 1,14	12,09± 3,61
	nighttime	3	3	4,93± 3,04	21,42± 9,45	23,04±11,37	27,62±18,07	77,01±32,56
Rhincalanus nasulus and *R. cornutus*	daytime	3	11	10,88± 2,09	1,69± 0,51	1,06± 0,06	6,16± 3,68	19,79± 1,33
	nighttime	2	9	22,75± 6,65	75,00±12,00	50,02± 2,35	18,38±10,39	166,15±26,74
Feeding on nutrients of plant origin (1.6 hours during the day and 0.7 hours at night)								
Undinula darwini	day	3	10	18.76±8,78	9,59± 3,11	15,17± 5,26	6,22± 3,18	49,74±20,89
	night	3	19	7,72±3,25	5,82± 2,55	5,90± 2,53	1,41± 1,10	20,85± 9,16
Pleuromamma abdominalis	day	4	11	5,40±2.02	0,78± 0,27	7,32± 2,32	0,43± 0,12	13,93± 3,20
	night	5	6	5,33±1,18	13,60± 3,36	4,38± 0,84	8,04± 3,28	31,35±10,19
Candacia aethiopica	day	3	10	0,36±0,06	0,29± 0,08	0,56± 0,16	0,18± 0,07	1,39± 0.49
	night	2	9	0,61±0.37	0,40± 0,06	3,98± 2,17	0,52± 0,18	5,50± 2,05
Euchaeta marina	day	6	9	0,30±0.11	1,53± 0,41	0,28± 0,08	0,34± 0,22	2,43± 0,44
	night	1	15	0,13	0,80	6,67	0,10	7,70
Oncaea sp.	day	1	23	1,56	0,40	15,21	0,44	17,61
	night	3	17	0,56±0,19	0,30± 0,14	1,09±0,56	0,18± 0,18	2,14± 1,00
Rhincalanus nasutus and *R. cornutus*	day	3	10	1,17±0,65	0,48± 0,28	1,13±0,32	0,82± 0,22	3,60± 0,58
	night	3	11	0,15±0,04	3.30± 0,95	5,72±3,61	0,92± 0,18	10,09± 4,28
Feeding on bacteria (1.6 hours during the day and 0.7 hours at night)								
Undinula darwini	day	3	10	2,10±0,91	1,03± 0,21	3,34±1,29	0,33± 0,07	6,81± 1,71
	night	3	14	6,27±0,64	2,77± 0 14	5,31±0,61	0,43± 0,23	14,73± 0,76
Pleuromamma abdominalis	day	3	8	0,98±0.36	1,30± 0,91	1,37±0,16	0,54± 0,04	4,19± 0,81
	night	5	5	2,05±0,72	13,85± 3,83	10,46±2,65	0,72± 0,19	27,08± 6,93
Candacia aethiopica	day	2	14	0,14±0,06	0,08± 0,04	0,23±0,007	0,01± 0.007	0,45± 0,11
	night	3	11	0,14±0,02	0,07± 0,06	0,57±0,22	0,02± 0,004	0,74± 0,23
Euchaeta marina	day	3	10	0,28±0,03	0,71± 0,45	0,98±0.48	0,36± 0,15	2,34± 0,73
	night	2	14	0,28±0,08	0,80± 0,36	1,03±0,54	0,009± 0,007	2,20± 1,22
Oncaea sp.	day	1	30	0,04	0,03	0,09	0,27	0,43
	night	3	24	0,17±0,05	0,13± 0,09	0,12±0,02	0,36±0,15	0,78± 0,49
Rhincalanus nasutus and *R. cornutus*	day	4	11	1,39±0.78	1,08± 0,15	3,48±2,08	0,20±0,06	6,16± 2,64
	night	3	8	0,46±0,07	1,18± 0,50	8,48±2,83	0,42±0,16	10,54± 3,40

Table 2

Daily indices of food balance (C_d - accumulation in the body, R_c - respiratory cost, U - assimilated substance, R_s - feces, R_d - excreted dissolved organic substance, F - unassimilated substance, R - ration) in abundant tropical copepods foraging on mixed food (cal and % of body weight) at t = 27-28°C

Species	Size, mm	Weight cal	Period of observation	No. of experiments	No. of animals per experiment	C_d cal/ind × 10^{-3}	C_d %	R_c cal/ind × 10^{-3}	R_c %	U cal/ind × 10^{-3}	U %	R_s cal/ind × 10^{-3}	R_s %	R_d cal/ind × 10^{-3}	R_d %	F cal/ind × 10^{-3}	F %	R cal/ind × 10^{-3}	R %	$\frac{U}{R}\cdot100$ %	Food requirements cal/ind	Food requirements %
Undinula darwini	2,42	0,293	day	9	10	30,423	10,4	21,105	7,2	51,528	17,6	26,919	9,2	11,169	3,8	38,088	13,0	89,616	30,6	57		
	2,2	0,22	night	9	14	40,224	18,3	37,972	17,7	79,195	36,0	34,827	15,8	9,241	4,2	44,068	20,0	123.263	56,0	64		
	2,3	0.251	24 hrs	18	12	70,647	28,1	60.077	23.9	130,723	52,0	61,746	24,6	20,410	8,1	82,156	32,7	212,879	84,8	61	0,0507	20
Pleuromamma abdominalis	4,33	1,519	day	10	9	10,406	0,7	43,241	2,8	53,648	3,5	9,302	0,6	6,515	0.4	15.817	1,0	69,465	4,6	77		
	4,11	1,29	night	13	5	20,368	1,6	309,698	24,0	330,087	25,6	138,461	10,7	70,861	5,5	209,322	16,2	539,409	41,8	61		
	4,2	1,417	24 hrs	23	7	30,794	2 2	352,939	24.9	383,735	27,1	147,763	10,4	77,376	5,5	225.139	15,9	608.874	43.0	64	0.2077	15
*Candacia aethiopica**	2,2	0,347	day	10	10	4,427	1,3	3,542	1,0	7,969	2,3	5,267	1,5	21,785	6,3	27,052	7,8	35,021	10,1	23		
	2,4	0,451	night	9	11	5,982	1.3	41,328	9,2	47,320	10.5	17,655	3,9	21,258	4,7	38,913	8,6	86,204	19,1	55		
	2,33	0.413	24 hrs	19	11	10.409	2,5	44.860	10,9	55,289	13,4	22,212	5,5	43.043	10,4	65,955	16.0	121.225	29.4	46	0.1014	24
Euchaeta marina	3,0	0,544	day	15	9	10,612	1,9	4,109	0,7	14,721	2,4	4,603	0,8	25,541	4,7	30,144	5,5	44,865	8,2	33		
	3,1	0,600	night	8	10	55,192	9,2	70,559	11,7	125,75	20,9	49,790	8,3	16,117	2,7	65,907	11,0	191,659	31,9	66		
	3.05	0,572	24 hrs	23	10	65,804	11,5	74,668	13,1	140,47	24,5	54,393	9,5	41,658	7,3	96,051	16,8	236.524	41.3	59	0.1604	28
Oncaea sp	1.17	0,071	day	4	30	1,623	2,3	2.073	2,9	3,696	5,2	14,070	19,8	2.243	3.1	16,314	22,9	20,010	28,1	18		
	1,12	0,062	night	9	21	4,804	7,7	16,347	26,3	21,150	34,1	19,228	31	22,242	35,8	41,471	66,8	62,621	101,0	34		
	1.14	0,065	24 hrs	13	25	6.427	9,9	18.420	28,3	24,846	38,2	33,298	51	24,485	37,6	57,785	88,9	82,631	127,1	30	0,0122	19
Rhincalanus nasutus and *R. cornutus*	3,4	0,776	day	10	11	6,781	0,8	2.008	0.2	8,789	1,1	4,241	0,5	3,486	0,4	7,727	1,0	16,516	2,1	53		
	3,0	0,533	night	8	9	17.615	3,3	62,142	11,6	79,757	15,0	59,945	11,2	15,620	2,9	75,573	14,2	155,330	29,1	51		
	3,2	0.646	24 hrs	18	10	24,396	3.8	64 150	9,9	88,546	13,7	64,186	9,9	19.116	2,9	83,300	12,9	171,846	26,6	52	0,0388	6

* The animals were active, but foraged lightly in some of the experiments.

Composition of the daily ration of abundant copepod forms (cal and % of total ration) from tropical zones of the Pacific Ocean (when feeding on mixed food - animal organisms, algae and bacteria) at t = 27-28°C

Species	Size, mm	Weight, cal	Composition of mixed nutrients	Concentration of food, cal/l	Inverse specific activity $C_r \times 10^{-6}$	C_a cal	C_a %	R_e cal	R_e %	U cal	U %	R_s cal	R_s %	R_d cal	R_d %	F cal	F %	R cal	R %	R, Body Weight %	$\frac{U}{R} \cdot 100$, %
Undinula darwini	2,3	0,251	Calanidae	1,8	1460,0	0,0304	14	0,0372	18	0,0676	32	0,0281	13	0,0120	6	0,0400	19	0,1077	51	43	63
			Amphidinium	0,374	6,5	0,0281	13	0,0175	8	0,0456	21	0,0222	10	0,0074	4	0,0296	14	0,0752	35	30	61
			Bacteria	0,164	5,3	0,0121	6	0,0054	2	0,0175	8	0,0115	5	0,0010	0,5	0,0125	6	0,0300	14	12	58
Pleuromamma abdominalis	4,2	1,417	Calanidae	2,5	400,0	0,0134	2	0,3059	50	0,3193	52	0,1161	19	0,0621	10	0,1783	29	0,4976	82	35	64
			Amphidinium, *Glenodinium*	0,337	14,4	0,0132	2	0,0231	4	0,0363	6	0,0132	2	0,0135	2	0,0268	4	0,0632	10	4,4	57
			Bacteria	0,460	5,4	0,0042	0,7	0,0239	4	0,0271	5	0,0184	3	0,0016	0,3	0,0200	3	0,0481	8	3,4	56
Candacia aethiopica	2,33	0,413	Calanidae	2,7	1100,0	0,0088	7	0,0439	36	0,0527	43	0,0147	12	0,0420	35	0,0567	47	0,1094	90	26	48
			Amphidinium	0,257	24,2	0,0013	1	0,0009	0,7	0,0022	1,7	0,0070	6	0,0010	1	0,0080	7	0,0102	8,7	2,5	21
			Bacteria	0,297	6,5	0,0003	0,3	0,0001	0,07	0,0004	0,3	0,0011	0,9	0	0,03	0,0012	0,92	0,0016	1,3	0,4	26
Euchaeta marina	3,05	0,572	Calanidae	2,5	528,0	0,0647	27	0,0702	30	0,1348	57	0,0406	17	0,0408	17	0,0814	34	0,2163	91	33	62
			Amphidinium	0,157	11,3	0,0005	0,2	0,0026	1,2	0,0030	1,4	0,0112	4,8	0,004	0,2	0,0117	5	0,0147	6,4	2,6	21
			Bacteria	0,318	6,4	0,0007	0,3	0,0019	1	0,0026	1,3	0,0025	1	0,0004	0,2	0,0029	1,3	0,0055	2,6	0,9	47
Oncaea venusta	1,14	0,065	Calanidae	2,2	246,0	0,0039	5	0,0174	21	0,0213	26	0,0183	22	0,0218	26	0,0402	48	0,0614	74	94	35
			Amphidinium	0,339	10,9	0,0022	3	0,0008	1	0,0030	4	0,0143	17	0,0006	1	0,0149	18	0,0180	22	28	17
			Bacteria	0,391	5,6	0,0003	0,4	0,0002	0,3	0,0005	0,7	0,0007	0,8	0,002	2,5	0,0027	3,3	0,0032	4	5	17
Rhincalanus nasutus and *R. cornutus*	3,2	0,646	Calanidae	2,2	412,0	0,0213	12,4	0,0555	32	0,0768	45	0,0370	22	0,0161	9	0,0530	31	0,1298	76	20	59
			Amphidinium	0,314	13,2	0,0012	0,7	0,0058	3	0,0079	4	0,0104	6	0,0022	1	0,0125	7	0,0196	11	3	36
			Bacteria	0,422	5,0	0,0019	1	0,0028	2	0,0047	3	0,0168	10	0,0008	0,5	0,0177	10	0,0225	13	3,5	21

Table 4

Daily energy balance in female tropical copepods when foraging on macroalgae from a mixture of food items (cal x 10^{-3} and % of body weight) at t = 27-28°C

Species	Size, mm	Weight, cal	Type of food	Concentration of food cal/l	No. of animals in experiment	C_d		R_c		U		R_s		R_d		P		R		$\frac{U}{R} \times 100$, %
						cal × 10^{-3}	%	cal × 10^{-3}	%	cal × 10^{-3}	%	cal × 10^{-3}	%	cal × 10^{-3}	%	cal × 10^{-3}	%	cal × 10^{-3}	%	
Euchaeta marina	3,0	0,517	*Streptotheca* Bacteria Calanidae	0,243 0,0028 1,98	10	2,225	0,4	0,788	0,15	3,014	0,6	1,423	0,27	0,630	0,12	2,073	0,4	5,087	1,0	59
Oncaea venusta	1,0	0,044	*Streptotheca* Bacteria Calanidae	0,243 0,0028 1,98	24	1,387	3,0	0,205	0,5	1,592	3,6	9,630	22	0,462	1,0	10,092	23	11,689	27	14
Pleuromamma abdominalis	4,2	1,417	*Streptotheca* Calanidae	0,243 0,0028 1,98	8	303,768	21	207,792	15	511,560	36	62,424	4,4	33,336	2,4	96,760	6,7	607,320	43	84
Candacia aethiopica	1,6	0,134	*Streptotheca* Calanidae	0,243 0,0028 1,98	8	0,600	0,4	7,080	5,3	7,680	5,7	25,080	19	14,880	11	39,960	30	47,640	36	16

*Three experiments were carried out for each species.

Electivity (E) in the feeding of abundant forms of tropical copepods

Species	Time of day	Type of food	Concentration of food in medium cal/1	Ratio of each food type in medium, A_c, %	Daily intake of food, cal/specimen	Relative importance of each food in ration, A_n, %	$E = \frac{A_n - A_c}{A_n + A_c}$
Undinula darwini	Day-time	Animal	0,78	44	0,043189	48	+0,043
		Algae	0,70	39	0,040836	46	+0,032
		Bacteria	0,31	17	0.005591	6	—0,48
	Night time	Animal	1,41	66	0.064474	52	—0,12
		Algae	0,41	19	0,034402	28	+0,19
		Bacteria	0,32	15	0.024387	20	+0,14
Oncaea sp.	Day-time	Animal	2,28	61	0,005199	26	—0,40
		Algae	0,63	17	0,014458	72	+0,62
		Bacteria	0,80	22	0.000353	2	—0,83
	Night time	Animal	1,38	53	0,056218	90	+0,26
		Algae	0,41	16	0,003515	6	—0,45
		Bacteria	0,80	31	0.002688	4	—0,77
Rhincalanus nasutus and R. cornutus	Day-time	Animal	1,53	63	0,008510	52	—0,096
		Algae	0,35	14	0,002956	18	+0,12
		Bacteria	0,56	23	0,005050	30	+0.13
	Night time	Animal	2.62	65	0.121311	78	+0,091
		Algae	0,41	10	0,016649	11	+0.05
		Bacteria	1.03	25	0,017391	11	—0.39
Pleuromamma abdominalis	Day-time	Animal	1.80	57	0,054588	79	+0.15
		Algae	0,45	14	0,011437	16	+0,07
		Bacteria	0,90	29	0.003440	5	—0,71
	Night time	Animal	3,93	72	0,443000	82	+0,06
		Algae	0,41	7	0.051727	10	+6.18
		Bacteria	1,13	21	0.044682	8	—0,45
Candacia aethiopica	Day-time	Animal.	2,85	72	0,033501	96	+0,14
		Algae	0,39	10	0.001142	3	—0,54
		Bacteria	0.70	18	0.000378	1	—0,89
	Night time	Animal	4,12	82	0,075920	88	+0,035
		Algae	0.31	6	0,009075	11	+0.29
		Bacteria	0,57	12	0.001209	1	—0.85
Euchaeta marina	Day-time	Animal	2,62	85	0.040957	91	+0,034
		Algae	0.012	1.0	0.001995	4.4	+0,63
		Bacteria	0.42	14	0.001913	4.3	—0,53
	Night time	Animal	3.56	81	0.175324	91	+0,058
		Algae	0,41	9	0,012705	7	—0.12
		Bacteria	0,42	10	0,003630	2	—0,67