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Duration of digestion in marine copepods

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Duration of digestion in marine copepods

by

Ye. G. Arashkevich

One of the most important problems of marine ecology is the problem of the quantity of food consumed by animals. There exist several methods for determining this quantity: by the quantity of food accumulated in the gut, by the level of radioactivity in the body of an animal fed on labeled food, or by the sum of the elements in a balance equation. In all these cases, it is essential to know the length of time the food takes to pass through the gut of the animal and the dependence of this value on the hour of the day and the concentration of food. 351*

* Numbers in the right-hand margin are those of pages in the original. - Trans.

MATERIAL AND METHODS

Food moves through the gut of copepods in the following way (Fig. 1): From the mouth, it enters the pharynx or fore-intestine, and immediately moves on to the secretory anterior section of the mid-gut. Here the food is retained for 10 - 20 minutes, depending on the degree of fullness of this section. One can easily see through the body covering of the copepod how the walls of plant cells are broken down and their contents released into the gut cavity. The gut walls contract peristaltically, and the contents of the gut are gradually mixed. After a while peristalsis intensifies, the valve separating the anterior section of the mid-gut from the posterior section opens, and part of the contents of the anterior section ($> \frac{1}{3}$) passes through to the posterior, absorptive section, where the feces are formed. The next intensification in gut peristalsis results in the opening of the valve between the mid-gut and the posterior gut. The fecal aggregate passes into the posterior gut and, without lingering there, leaves the gut. Immediately after discharge of the feces, the valve that divides the mid-gut into two sections opens and the next portion of food enters the absorptive section of the mid-gut. Since entomostracans feed at a relatively constant rate, the working of their gut is very rhythmical. Intensive peristaltic contractions resulting in the expulsion of feces and the passing of food from one section to another occur at equal time intervals. The frequency of these contractions and, consequently, the rate of discharge of feces, varies from one individual to another of the same species and depends, evidently, on the physiological condition of the animal.

To determine the time taken by food to pass through the gut, either the visual method (Petipa, 1959) or the method using food labeled with C^{14} (Sorokin, 1966) is usually employed. The essence of the methods using C^{14}

is as follows. First method: entomostracans are fed labeled food for 3 - 5 min. and then, after [excess] labeled food is washed off them, transferred to a vessel containing unlabeled food. The feces are taken out at regular intervals and their level of radioactivity is determined. Digestion time is established on the basis of the length of time taken by the C^{14} to appear in the feces. In the second method, entomostracans are kept on labeled food until their guts are completed filled. After washing, the animals are successively transferred, at 10 - min intervals, to a new vessel containing unlabeled food. The water in the vessels from which the

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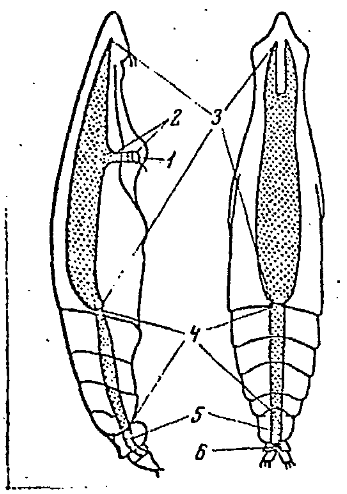

Рис. 1. Схема пищеварительного тракта *Eucalanus attenuatus*

1 — ротовое отверстие; 2 — глотка; 3 — передний отдел средней кишки; 4 — задний отдел средней кишки; 5 — задняя кишка; 6 — анус

Fig. 1. Plan of the digestive tract of *Eucalanus attenuatus*

1. mouth opening; 2. pharynx; 3. anterior section of mid-gut; 4. posterior section of mid-gut; 5. posterior gut; 6. anus.

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copepods have been removed is drained through a diaphragm filter (we used a No. 3 filter), and the radioactivity of the feces remaining on the filter is determined. The digestion time of the food is established on the basis of the time taken by the C^{14} to disappear from the feces. In work with marine copepods, both methods proved to be not always applicable and required some supplementation.

The first method was used to determine speed of digestion in the marine copepod *Acartia tonsa* (Fig. 2). In both experiments, two peaks in the discharge of radioactive feces - 25 and 50 min after the end of feeding with labeled food - were observed. It is possible that some of the animals reacted negatively to the transfer from one aquarium to another or were traumatized during the washing, and defecated prematurely. However, such explanations do not help in determining digestion time more precisely. Our observations indicated that tropical marine copepods require a long time to adapt to the conditions of experimental feeding; therefore we had to reject the short-term feeding method.

The second method - determination of digestion time by the rate of discharge of radioactive feces - was used in two modified forms. In the first, we transferred the animals fed on labeled food from one aquarium to another, and then filtered the water. In a number of cases, for example with *Clausocalanus mastigophorus* (Fig. 3), *Pleuromamma xiphias* and *Eucalanus subtenuis*, good results were obtained by this method, but with most marine copepods it too proved unsuitable. Some animals react so badly to the constant transfers from one vessel to another that they stop eating and discharging feces after the third or fourth transfer. The difficulty of capturing individuals quickly for transfer makes it impossible to use a large number of animals in the experiments. This considerably lowers the accuracy of determinations made for large entomostracans, and makes the method unsuitable for small ones. Various species react differently to changed

Рис. 2. Определение времени переваривания пищи (*Prorocentrum*) у *Acartia tonsa* по появлению радиоактивности в фекалиях (два опыта)

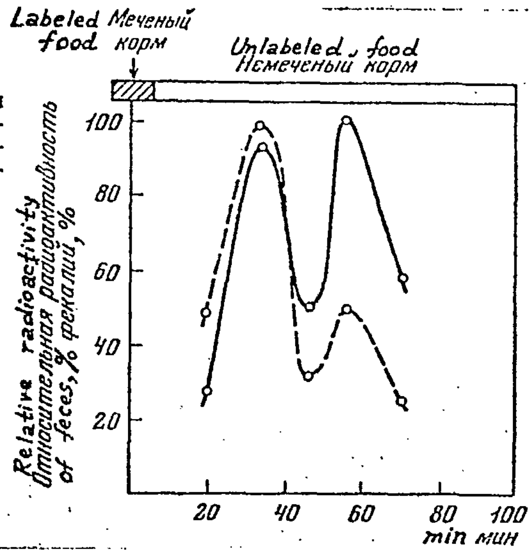

Fig. 2. Determination of digestion time (of *Prorocentrum*) in *Acartia tonsa* by onset of radioactivity in feces (two experiments)

Рис. 3. Определение времени переваривания пищи (*Streptotheca*) у *Clausocalanus mastigophorus* по скорости выделения радиоактивных фекалий

1, 2 — дневные опыты; *3* — ночной опыт

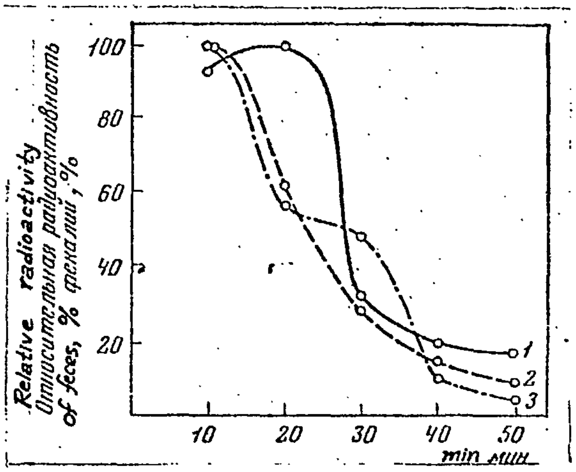

Fig. 3. Determination of digestion time (of *Streptotheca*) in *Clausocalanus mastigophorus* by the rate of discharge of radioactive feces

1 and 2. daytime experiments; 3. nighttime experiment

Рис. 4. Определение времени (в трех опытах) переваривания пищи (*Prorocentrum*) у *Acartia tonsa* по скорости выделения радиоактивных фекалий (*а*) и по уменьшению радиоактивности в отдельных фекальных комочках (*б*)

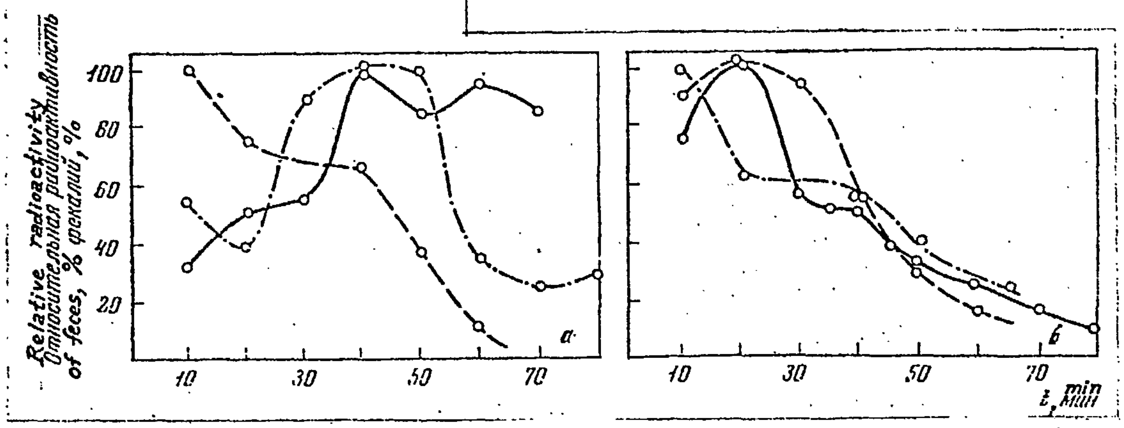

Fig. 4. Determination (in three experiments) of digestion time (of *Prorocentrum*) in *Acartia tonsa* by the rate of discharge of radioactive feces (a) and by the decrease of radioactivity in separate fecal aggregates (b).

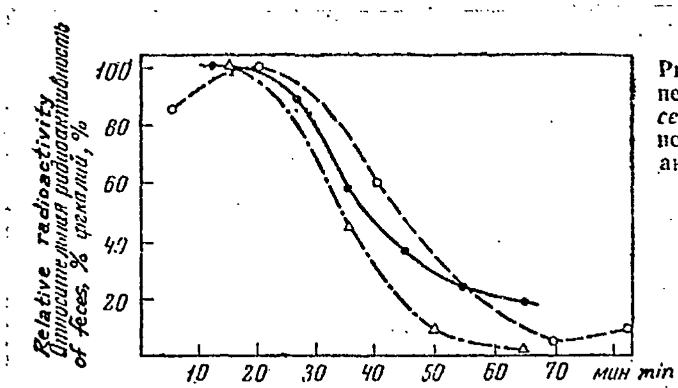

Рис. 5. Определение времени переваривания пищи (*Prorocentrum*) у *Eucalanus attenuatus* по скорости выделения радиоактивных фекалий

Fig. 5. Determination of digestion time (of *Prorocentrum*) in *Eucalanus attenuatus* by the rate of discharge of radioactive feces.

conditions and mechanical irritation [or stimulation. - Trans.]: in some cases defecation speeds up, while in others it is considerably retarded. During an uneven rate of discharge of feces, when an entomostracan, in an adaptation period occupying the first 30 min, discharges very few feces, a picture of changing radioactivity on the filters such as that shown in Fig. 4a is obtained. It is very difficult to judge the speed of disgestion from such a curve. In order to avoid such complications we placed the animals, after they had been washed of labeled food, in a Petri dish with a ruled bottom and removed the feces under a microscope. Then we counted the number of feces discharged over each ten-minute period and determined their radioactivity. Digestion time was also judged by the speed with which the labeling disappeared. Estimation of the amount of feces for each specimen makes it possible to evaluate the radioactivity of each fecal aggregate, and obtain a picture of the change of this value due to time that is sharper and closer to the theoretical one (Fig. 4b). It is not yet known what influence the constant, intensified lighting on the microscope stage has on the feeding behavior of entomostracans. However, Yu. A. Rudyakov's experiments (1974) showed that when the light is greatly increased, the motor activity of copepods and ostracods increases sharply at first, but returns to the previous level in as little as five minutes. This makes it possible to assume that there was no significant change in the feeding activity of entomostracans under the experimental conditions described above. With copepods that produce large feces, for example *Eucalanus attenuatus*, the radioactivity of each fecal aggregate was measured and the time of its discharge was recorded (Fig. 5).

In our work we mainly used the second modification of this method.

BASIC FINDINGS

Digestion time was studied in copepods belonging to two trophic groups: filterer-phytophagans (Calanidae and Eucalanidae) and euryphages with a mixed method for obtaining food (Pseudocalanidae, Metridiidae, Scoleci thricidae, Centropagidae and Acartiidae). Both groups consume plant food intensively in the absence of other types of food. For food we used peridiniaceous and diatomaceous algae measuring 11 - 64µ , in concentrations of 0.5 - 3 mg of food per liter. In terms of duration of digestion (Table 1), the copepods that were studied can be divided into three categories: those with a digestion time of 30 - 40 min (*N. gracilis, R. nasutus, C. mastigophorus, P. xiphias, E. subtenuis, R. cornutus*), 50 - 60 min (*E. attenuatus, A. tonsa*) and 75 - 125 min (*N. minor, S. danae, Centropages* sp.). All three categories contain both phytophagans and euryphages, so that attempts to establish a connection between the nature of the diet of entomostracans and their duration of digestion are unsuccessful. The same applies to the connection of duration of digestion in entomostracans with their body size and depth of habitation.

The rate of passage of food in *E. attenuatus* and *A. tonsa*, lower than in most of the copepods studied at a food concentration of 1 - 3 mg/1, is possibly connected with the adaptation of these entomostracans to high concentrations of food under natural conditions. This is more obvious in *A. tonsa*, which inhabits the rich phytoplankton area of the Peruvian coastal upwelling, than in *E. attenuatus*, which is found in more oligotrophic areas. In these copepods, a decrease in duration of digestion was traced when the food concentration was increased from 50 - 60 min at a concentration of 1 - 3 mg/1 to 30 - 40 min at a concentration of 10 mg/1

Table 1

Duration of digestion in tropical copepods at temperatures of 17 - 19°C

Таблица 1

Продолжительность переваривания пищи у тропических копепод при температуре 17—19°

Вид потребителя Consumer species	Вид корма, концентрация Food species, concentration	Число опытов No. of experiments	Продолжительность переваривания пищи, мин Duration of digestion, min.
Neocalanus gracilis	*Amphidinium*, 2 мг/л	3	33
Rhincalanus nasutus	То же Ibid.	2	35
	Prorocentrum, 2 мг/л	2	40
Clausocalanus mastigophorus	*Streptotheca*, 0,5 мг/л	4	30
	Streptotheca, 1 мг/л	2	35
Pleuromamma xiphias	*Streptotheca*, 3 мг/л	3	28
Nannocalanus minor	*Prorocentrum*, 1 мг/л	3	75
Scolecithrix danae	То же Ibid.	2	120
Centropages sp.	*Gyrodinium*, 2 мг/л	2	125
Eucalanus subtenuis	*Prorocentrum*, 1 мг/л	2	35
	Prorocentrum, 3 мг/л	2	30
	Gymnodinium, 1,5 мг/л	1	40
	Streptotheca, 1,5 мг/л	2	35
Eucalanus attenuatus	*Prorocentrum*, 1 мг/л	5	55
	Prorocentrum, 3 мг/л	3	50
	Prorocentrum, 10 мг/л	2	30
Acartia tonsa (?)	*Prorocentrum*, 1 мг/л	5	55
	Prorocentrum, 2 мг/л	3	60
	Prorocentrum, 10 мг/л	2	37

(Table 1). Experiments in determining the dependence of the size of the ration on concentration, conducted on *A. tonsa* (Petipa et al, 1975), showedthat when the food concentration is increased from 1 to 10 mg/1, the ration nearly doubles. Connecting these data with our findings on the speed of food passage, it can be presumed that when concentration

Table 2

Duration of digestion in copepods at various times of the day, at temperatures of 17 - 19°C

Таблица 2

Продолжительность переваривания пищи у копепод в разное время суток при температуре 17—19°

Вид потребителя Consumer species	Время суток, час Time of day, hrs.	Число опытов No. of experiments	Продолжительность переваривания, мин Duration of digestion, min.
Neocalanus gracilis	14—18	2	30
	00—02	1	40
Rhincalanus nasutus	17—19	1	30
	23—01	1	40
Rh. cornutus	00—03	2	40
Clausocalanus mastigophorus	12—14	3	20
	01—05	3	25
Pleuromamma xiphias	13—16	2	30
	02—04	1	25
Nannocalanus minor	00—02	1	70
	14—16	2	75
Scolecithrix danae	17—19	1	120
	01—03	1	90
Centropages sp.	17—19	1	120
	01—03	1	130
Eucalanus subtenuis	12—15	2	30
	19—21	2	35
	22—23	2	40
	00—02	2	30
E. attenuatus	13—17	2	65
	18—22	3	40
	00—05	4	45
Acartia tonsa (?)	10—12	1	60
	14—17	3	53
	17—19	2	37
	20—22	3	43
	00—02	2	35

increases the assimilability of the food decreases, and the amount of food assimilated remains relatively constant.

The long duration of digestion in copepods of the third category can probably be explained in terms of the physiological condition of the population: during the experiment, females of *Centropages* sp. and *N. minor* began laying eggs. Unfortunately, a lack of sufficent material made it impossible to repeat the experiments with *S. danae* using visual observation.

Over a 24-hour period, no perceptible change in digestion speed was noted in most of the entomostracans (Table 2). This agrees with the data on the absence of a daily rhythm of food consumption that were obtained on this voyage by T. S. Petipa et al. (1975). An exception is presented by *E. attenuatus* and *A. tonsa*, in which a tendency toward an increase in duration of digestion is noted during daylight hours (55 - 65 min in the daytime, 35 - 45 min at night). Intensity of food consumption in *Eucalanus* was higher at night than in the daytime (Petipa et al., 1975). Unfortunately, there are no figures on the daily rhythm of feeding rates of *A. tonsa*.The direct connection which we noted between the rate of feeding and the rate of discharge of feces suggests that in this case as well the entomostracan tries, when there is a rise in the quantity of food consumed, to keep constant the amount of food assimilated - if we assume that this amount is directly proportional to the digestion time. But in this case it is incomprehensible what makes copepods increase their rate of food consumption in the evening and at night, unless this results from differences in the speed and degree of adaptation to experimental conditions of entomostracans captured at various times of the day and at various depths.

CONCLUSIONS

A comparative study of existing methods for using C^{14} in determining rates of food passage showed that when working with tropical marine copepods visual observation of the behavior and condition of the experimental animals is essential, as is estimation of the number of feces discharged per unit of time.

Different copepods have different rates of digestion of plant food, and these differences are connected with neither the method of feeding nor the size nor the depth of habitation of the entomostracans. Apparently, they are explained by the physiological peculiarities of a population.

Over a 24-hour period no significant change in digestion rate was seen in most of the entomostracans. The exceptions were *E. attenuatus* and *A. tonsa*, in which the digestion period increases noticeably in daytime.

When the concentration of food increases, the ration grows and the rate of digestion increases. This leads to a reduction in the assimilability of the food and helps to keep the quantity of food assimilated on a single level.

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DURATION OF FOOD DIGESTION IN MARINE COPEPODS

E. G. Arashkevich

Summary

A comparative study was made of methods for determining the duration of food digestion in marine copepods using ^{14}C. The rate of passage of vegetable food was investigated in 11 copepod species. Differences in digestion rate do not depend on food habits, nor size and depth of habitat, and seem to be accounted for solely by the physiological peculiarities of the population. In most of the copepods investigated digestion rate did not change during the 24-hours period but in Eucalanus attenuatus and Acartia tonsa a tendency was noted to an increase in the rate of food passage during night hours. The rate of digestion decreases with increasing concentration of food.