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Paper No. 4 from 'Structure and dynamics of aquatic communities and populations'

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Food utilization and energy conversion by Black Sea Cladocera populations

In the upper layers of the Black Sea, down to the thermocline, lives a warmth-loving epiplanktonic ~~organism~~ animal ~~complex~~ which, by its composite species, reaction to temperature, and other factors of the environment, can be looked upon as an independent community of pelagic life. It has been pointed out in the literature that this planktonic community shows condiderable seasonal variability as to composition and numerical significance (Petipa, Sazhina, Delalo, 1960). In the summer, great numbers of the species group Cladocera keep developing along with the warmth-loving Centropages kröyeri and Acartia latisetosa which disappear with the insetting cold. The aim of the present

paper is to study the role of Cladocera within the indicated community.

Many investigators of the Black Sea zooplankton have pointed out that Cladocera are developing in great quantities during the warm season, both in the litoral and in the open waters of the Black Sea (Zernov, 1913; Kusmorskaya, 1950; Dolgopol'skaya, 1958; Pavlova, 1961, and others). Table 1 presents data concerning the relative importance of Cladocera in the numerical quantity and the biomass of zooplankton in the epiplanktonic complex of the various Black Sea regions and for different years. In the coastal waters, as is evident from the table, Cladocera represent up to 70% of the general biomass and in the central regions of the Black Sea up to 22%. Out of seven Black-Sea Cladocera species described so far, only four are found with appreciable frequency: Penilia avirostris D a n a , Evadne spinifera M ű l l e r, E. tergestina C l a u s , and Podon polyphaemoides L e u k .

Most outstanding as to their mass are Penilia avirostris (table 1). Essentially, owing to this species, the general number and the biomass of Cladocera increase in the litoral waters within the epiplankton community. The numbers of the two species of Evadne are slightly increasing from the sea shore towards the open waters. During the summer, Acartia clausi G i e s b r., also an epiplanktonic species, represents up to 20% of the general biomass in this community of the open waters. One should probably consider P. avirostris (67)

and A. clausi, along with Oithona minuta, to be the predominant species among the upper-layer plankton complex in the Black Sea.

T a b l e 1

Importance of ~~massive~~ Cladocera species in the epiplankton community of the Black Sea in August (in % of the over-all numbers and the biomass of zooplankin the 0 - 20 m layer)

Species	North-west. region 1957		Crimean coast 1951		Central region 1951		Central region 1957	
	numbers	biomass	numbers	biomass	numbers	biomass	numbers	biomass
Penilia avirostris	18,2	60,2	11,3	42,2	5,6	17,0	5,4	5,2
Evadne spinifera	2,8	8,6	0,6	1,7	1,1	3,4	8,1	8,7
Evadne tergestina	0,3	0,9	0,5	1,4	0,5	1,7	2,9	3,1
Podon polyphaemoides	0,09	0,05	0,03	0,002	0,02	0,01	0	0
T o t a l	21,4	69,7	12,4	45,3	7,2	22,1	16,4	17,0

The nutritive value of Cladocera is considerable. On the average, their body contains up to 63% albumen and 12,8% fat in relation to raw weight. The huge numbers and the high calorie content of these organisms attract large shoals of plankton-eating fish to places where Cladocera swarm (Shmeleva, 1958; Koval', 1965, and others); and for fish larvae they, sometimes, represent an essential part of the food ration (Pavlovskaya, 1958; Duka, 1959; Sinyukova, 1964, and others).

In consideration of the above data, it seems worthwhile to determine the role of the Cladocera group in the over-all

balance of matter and energy for the complex of plankton organisms in the Black Sea surface waters.

In order to obtain the food ration quantities by indirect methods, without possessing data about the food actually consumed by the organism, one mostly utilizes the balance equality according to which the ration energy, at a determined percentage of food assimilability, equals the sum of growth energy and metabolism energy. Energy expended in the metabolism process was computed from the quantities of utilized oxygen and the magnitudes of growth energy were obtained on the basis of experimental data for a 24-hour growth of an organism; by growth is meant the increase of the body mass within 24 hours without expenditure for reproduction, and in all of the following exposition, we shall use this term as indicated here. The positive possibility to calculate the nutritive ration on the basis of experimentally obtained quantities for (68)
oxygen utilization and body growth within a fixed period of time was demonstrated on the example of P. avirostris. The rations calculated by balance equality and those actually established for this species under natural and laboratory conditions turned out to be sufficiently close (Pavlova, 1964). Possessing average magnitudes for metabolism and growth within a 24-hour period, food rations for other ~~massive~~ important Cladocera groups encountered in the Black Sea can be calculated.

Determining the 24-hour rations

Energy expenditure for metabolism was determined on

the basis of oxygen utilization for three Cladocera species: Penilia avirostris, Evadne spinifera, and Podon polyphaemoides. The data for oxygen utilization intensity for the first two species were obtained in 1960 at the occasion of experiments conducted on board the research ship 'Akademik A. Kovalevsky' by the method of closed glass containers. Five to six times in a 24-hour period, the experimental containers were placed on a rope to a fixed sea level in order to determine the average daily quantity of oxygen utilization by a given species. For P. polyphaemoides, the experiments were conducted in stationary conditions in Skadovsky's apparatus (Shcherbakov, 1935). The water for the experiments was filtered through a porcelain filter catching all particles over bacteria size. Crustaceans of one species and size, with embryos in the egg stage, were put twice into pure water passed through the above-mentioned filter; then they were placed into the experimental container, 15 to 40 specimens at a time, depending on size. Exposure time was four hours. The oxygen was determined by Winkler's method in his micromodification. Container capacity was 35 to 42 ml. By means of Krogh's curve, the obtained data were reduced to 20° C.

The experiment results are tabulated on table 2. The eventual magnitudes of oxygen utilization for these species were calculated by the equation of G.G. Winberg for crustaceans: $Q = 0,2\ W^{0,81}$ at 20°, where Q is the quantity of utilized oxygen (in ml), W = weight of the organism (in g) Winberg, 1950).

The magnitudes of metabolism intensity computed by the equation and those determined factually for Black Sea Cladocera proved to be of the same order. As a consequence of keeping P. polyphaemoides for 24 hours in water without additional food before the experiment, metabolism intensity for this crustacean was twice as low as calculated by the equation. Due to working methods on the research ship for determining metabolism intensity, Penilia and Evadne were not kept in water for 24 hours before the experiment.

T a b l e 2 (69)

Metabolism intensity of Black Sea Cladocera at 20° C

Таблица 2

Интенсивность обмена черноморских кладоцер при 20° С

Вид Species	raw weight Сырой вес, мг mg	body length Длина тела, мм mm	no. of Количество измерений measurements	Потребление O_2, мг час$^{-1}$ Utiliz. mg hour: 1000 экз.	1 г сырого веса	raw wgh. 1 г сырого веса	1 г сух. в.	1000 ind.P. 1000 экз. по уравнению $Q=0.2\ W^{0.8}$ hour mg O_2 by above equation
Penilia avirostris juv.	0,005	0,44	9	0,011	0,002	2,20	0,28	0,016
Penilia avirostris ♀♀	0,032	0,75	21	0,065	0,009	1,99	0,30	0,072
Podon polyphaemoides	0,0093	0,37	16	0,012	0,001	1,56	0,29	0,027
Evadne spinifera	0,0194	0,70	7	0,054	0,014	2,95	0,76	0,048

The chemical composition of the ~~research~~ experimental organisms was determined in the hydrochemical laboratory of the Biology Institute of Southern Seas of the Ac. of Sciences of the Ukrainian SSR. It was as follows: for P. avirostris: albumen - 59,8, fat - 12,8, carbohydrates - 19,5, ashes - 7,9% per 1 g of dry weight, water - 85%; for P. polyphaemoides and

E. spinifera: albumen - 66,2, fat - 12,9, carbohydrates - 12,7, ashes - 9,2% on dry weight, water - 91,8%. Knowing the amount of oxygen required for the oxidation of 1 g of dry matter for a specific chemical composition, it is possible to calculate the quantity of matter which will be oxidized by the oxygen utilized by an organism of the given species within 24 hours. Calories were calculated from the chemical composition and gave the following results: for Penilia females - 5,46 kcal, for juveniles - 4,46 kcal; Podon and Evadne adults - 5,60 kcal, juveniles - 4,6 kcal per 1 g of dry matter. When computing the expenditure for metabolism, the usual coefficients of incomplete oxidation of organic matter were utilized: for albumen - 1,28, for fat - 2,88, for carbohydrates - 1,18.

Body mass accretion for 24 hours will consist of the amount in weight increase of the animal for 24 hours plus the organic matter going into the development of sexual products. In order to determine the amount of accretion, it is necessary to know the growth period and the difference between the initial and the final weight of an animal of each species. The weight of new-born young (the inital weight) and the duration of periods between the recurrent castings of skin for Penilia and Podon were determined experimentally. For Evadne's of average size, accretion was calculated by formulae taken from G. G. Winberg's writings (1966) and V.S. Ten and V.E. Zaika (1967): $\frac{dw}{dt} = kW_t\left[\left(\frac{W_\infty}{W_t}\right)^{1-\frac{a}{b}} - 1\right]$; $k = T\cdot\frac{K_2}{1-K_2}\cdot\frac{1}{W_t}\cdot\left(\frac{W_\infty}{W_t}\right)^{1-\frac{a}{b}-1}$,

where $\frac{dw}{dt}$ is weight accretion of the organism within a time unit, W_t is its initial weight, W_∞ - the final weight of the organism, K_2 - the coefficient of food utilization for growth, T - metabolism/of the organism at weight W_t. Calculating weight for Evadne by these formulae, it is assumed that W_∞ is equal to 0,035 mg of raw weight, W_t - 0,0194, T - 0,0147 mg of raw weight, and K_2 - 0,25 (as this was ascertained for Podon from experimental data). A preliminary computation for the accretion of adult Podon forms from these formulae showed that the calculated magnitudes and the ones established according to factual data were the same. Consequently, one can assume with a sufficient degree of certainty that the calculated accretion for Evadne will be close to the real one. According to these calculations, the 24-hour growth for adult Evadne specimens represents 0,0004 mg of dry weight. The initial data utilized for the calculation of weight accretion for all species are shown on table 3.

T a b l e 3

Increment of organic matter for 24 hours for Black Sea Cladocera during the period of active growth (calculated for one specimen)

Species	Weight f.l newborn ind. in mg of dry weight	Weight -female at sexual maturity	Weight -female at max. size	No. of moltings	Duration of ea. molt in hours, at 23 degr.C	Average no.of eggs in brood	Accretion of org.matter in mg of dry weight
P. avirostris	0,000240	0,00136	0,0051	5	45	8	0,00140
P. polyphaemoides	0,000059	0,00040	0,0019	7	48	4	0,00019
E. spinifera	0,000120	0,00060	0,0033	?	48?	3	0,00048

Since fully-formed juveniles are leaving the brood-pouch of Cladocera at every molting, the quantity of organic matter utilized for reproduction is equal to the weight of a new-born brood. The computed magnitudes of 24-hour rations for juvenile and adult specimens of Black Sea Cladocera as well as the correlation of metabolism, accretion and ration are presented on table 4. Unassimilated food amounts to 26% of the ration, analogous to what was established concerning the assimilation capability of P. avirostris (Pavlova, 1964).

The adduced calculations corroborate a point of view expressed more than once in the literature, namely that in natural conditions adult plankton crustaceans consume a great quantity of food, and that for many of them the 24-hour ration attains one hundred and more percent of their body weight (Cushing, ~~Vicetic~~ Vucetic, 1963; Petipa, 1964; Pavlova, 1964, and others). Water flea Cladocera which are less lively and move at a more even pace expend much less energy on metabolism in 24 hours than Copepods (Petipa, 1966). Nonetheless, a great part of the ration energy (32 - 49 %) and of the physiologically useful food (44 - 66%) are utilized for metabolism by Cladocera. The fact that the amount of oxygen utilization by marine organisms depends on the character and the speed of movement has been noted by many authors (Conover, 1960; Petipa, 1964; Pavlova, 1967, and others). Along with this, it is certain that the manner of feeding of (71)

a given animal influences oxygen utilization to a considerable degree. It has been noticed that predator crustaceans expend a great amount of oxygen not only for their searching and preying activity, but also for the assimilation of animal albumen (Conover, 1960). As to the investigated Cladocera, a greater energy expenditure for metabolism among the more mobile carnivorous species, i.e., Evadne, is clearly noticeable by comparison with Penilia and Podon, which swim slowly and eat plant food.

The major part of the physiologically useful ration is spent on accretion by sexually immature organisms (54%). Since sexually mature Cladocera simultaneously with molting and evacuating the recurrent brood lots continue to grow, up to 20% of the physiologically useable ration is expended on accretion by adult individuals. A considerable part of the nutritive ration goes into the developing of embryos which is quite in agreement with the accelerated tempo of parthogenetic reproduction; within 36 to 48 hours, Cladocera produce 3 to 8 specimens capable of an independent existence. Greater food rations during the reproduction period has been observed for marine Copepods, too (Marshall, Orr, 1952; Beklemishev, 1954; Petipa, 1959; Delalo, 1961). All in all, the body mass accretion within 24 hours for female Cladocera of an average size, including reproduction, is as follows: for Penilia - 58,6, for Podon - 46,9, and for Evadne - 33,8 % of the physiologically utilizable food.

These are the general rations in percentages of body weight for Black Sea Cladocera during the periods of their intensive reproduction: Penilia - 73, Podon - 71, and Evadne - 120. Since all calculations were obtained by proceeding from optimal requirements of an organism in food and energy, one should suppose that the adduced figures do not represent the maximal magnitudes of possible rations. Many investigators have noticed that, when great quantities of food are available in the sea, marine organisms of various kinds increase their optimal rations by several times (excessive feeding). However, Black Sea Penilia females, when experimentally fed with small floating flagellated algae up to 8 μ, showed that an increased quantity of cell consumption within a certain time unit does not exceed a definite limit. When in our experiments a concentration of algae up to 400/500 cells/ml was reached, the penilia's filtrating apparatus was soon clogged with the algae cells, (72) and the little creature, constantly cleaning it with its appendages, lowered the filtrating speed considerably. And when left in such a concentration for a longer time, the Penilias stopped filtrating altogether. Therefore, the magnitude of the food ration for Cladocera (particularly for Penilia avirostris) - at least when fed with algae - is restricted and, probably, cannot reach a considerable quantity (up to 370% of body weight), as is the case for Copepoda in conditions of food abundance (Cushing, 1964). On the other hand, Cladocera practically do not at all tolerate even starvation. Cladocera, twice carefully

Table 4

24-hour food requirement (in dry matter and calories) and the correlation of metabolism, accretion and ration for Black Sea Cladocera (in % of body weight, ration and its physiologically useful part)

Вид Species	weight Вес, мг mg	Калорийность caloricity	expenditure Затраты на обмен f.metabolism мг mg	кал cal	for accretion Затраты на прирост мг mg	кал cal	for reproduction Затраты на размножение мг	кал	food not utilized Неиспользованная пища мг	кал	general ration Общий рацион мг	кал	% веса тела	
Penilia avirostris														
females	0,0048	0,026	0,00114	0,0062	0,0004	0,00220	0,00100	0,0053	0,00020	0,0010	0,00350	0,01800	73	0,36
% of weight and body caloricity			23,7	23,8	8,3	8,4	20,8	20,4						
% of general ration			32,6	32,8	11,4	11,6	28,6	28,0						
% of physiologically useful ration part			44,8	45,7	15,6	16,0	39,3	38,7						
juveniles	0,0008	0,004	0,00016	0,0007	0,00019	0,00080	—	—	0,00012	0,0005	0,00047	0,0020	59	0,25
% of weight and body caloricity			20,0	17,5	24,0	20,0	—	—						
% of general ration			34,0	35,0	40,4	40,0	—	—						
% of physiologically useful ration part			45,7	46,6	54,2	53,3	—	—						
Podon polyphaemoides														
females	0,00976	0,004	0,00021	0,0012	0,00007	0,00038	0,00012	0,00067	0,00014	0,0008	0,00054	0,00306	71	0,31
% of weight and body caloricity			27,6	30,0	9,2	9,7	15,8	16,7						
% of general ration			38,8	39,2	12,9	12,7	22,2	21,9						
% of physiologically useful ration part			52,5	53,1	17,5	17,2	30,0	29,2						
Evadne spinifera														
females	0,00160	0,009	0,00095	0,0053	0,00030	0,00170	0,00018	0,00100	0,00035	0,0020	0,00193	0,1085	120	0,67
% of weight and body caloricity			59,3	58,8	18,7	18,8	11,2	11,1						
% of general ration			49,2	49,0	15,5	15,7	9,3	9,2						
% of physiologically useful ration part			66,4	66,2	20,9	21,2	12,6	12,5						

washed in sterilized water, were then placed into a vessel containing sterilized water. Under such conditions, the crustaceans lasted about 24 hours. Therefore, there must always be sufficient food in the sea to secure their normal ration. In this connection, an attempt was made to calculate the quantity of organic matter expended by Black Sea Cladocera in the open waters and near the coast during the time of their ~~massive~~ greatest development, and to establish the ratio of this quantity to the food at hand.

Food utilization by populations

Knowing the food quantity consumed by one crustacean within 24 hours during the period of active growth and reproduction affords the possibility to calculate the general amount of organic matter and energy expended by the whole population and for everyone of the different investigated species. For these calculations, the numerical data of Cladocera at hand in the month of August, contained in the materials of the synchronized Black-Sea surveys carried out by the Sevastopol Biology Station in 1951 and 1957 were utilized. The averages of Cladocera numbers according to species were obtained from single determinations at several (5 to 8) stations which tried to cover the whole region. The data concerning the eastern Black Sea were kindly put at the disposal of our organization by the hydro-biological laboratory of the Asov and Black Sea Fisheries Research Institute. Table 5 shows the

calculation of food consumption within 24 hours by Cladocera populations in the Black Sea. The 24-hour consumption by E. tergestina is considered to be equal to that of E.spinifera.

The highest numbers in all parts of the sea are those of Penilia populations which attain 95,000 specimens under 1 m^2 of the 0-to-20 m layer. Populations of the two Evadne species are much rarer, and Podon is altogether seldom found. Consequently, it is Penilia which utilizes the greatest part of organic matter and energy. Most favourable for the development of all kinds of Cladocera is the north-western region of the Black Sea (greater quantities of phytoplankton, drainage of detritus by the rivers); therefore, the utilization of organic matter and energy, falling to the share of Cladocera in that region of the sea, is the maximal one by comparison with other regions - 1263 cal within 24 hours (see table 5). Due to the (75) treating methods of the zooplankton samples taken by these synchronized surveys, the size of Cladocera was mostly not determined, and it is difficult to estimate the numbers of juveniles and adults. In order to determine this correlation, a counting of sexually immature and of adult Cladocera was carried out in the open waters of the Black Sea at one of the 24-hour stations (8 series); this was done from the 4th to the 5th September, 1960. The Penilia population revealed an average of 43% young within 24 hours, the populations of Evadne spinifera and E. tergestina - 12%. This ratio between adults and juveniles is assumed for the data on table 5.

Table 5

24-hour food utilization of Cladocera populations in the Black Sea during the month of August 1951 & 1957 (numbers - by individuals; utilization - in mg of dry matter & cal, below 1 m^2 of the 0 - 20 m layer)

Вид Species	Central region Центральный район						North-western region Северо-западный район			Eastern reg. open waters Восточный район (открытое море)			At Crimean coast У берегов Крыма		
	1951 г.			1957 г.			1957 г.			1957 г.			1951 г.		
	ind.	mg	kcal	ind.	mg	kcal	ind.	mg	kcal	ind.	mg	kcal	ind.	mg	kcal
Penilia avirostris															
Молодь young	13380	0,9	26,7	1030	0,5	2,1	40890	19,2	81,8	31390	14,7	62,8	25800	12,1	51,6
Самки females	17760	62,2	335,7	1370	4,8	25,8	54210	189,7	1024,5	41610	145,5	786,1	34200	119,7	646,4
Evadne spinifera и *E. tergestina*															
Молодь young	1040	0,3	1,2	580	0,2	0,7	1930	0,5	2,3	130	0,1	0,1	640	0,2	0,8
Самки females	7600	7,1	82,2	4320	8,3	46,6	14130	13,1	152,6	950	1,8	10,3	4730	9,1	51,1
Podon polyphaemoides	90	0,1	0,2	0	—	—	460	0,2	1,4	—	—	—	20	0,1	0,1
Итого Total	39870	70,5	446,0	7300	13,8	75,2	111620	222,7	1262,6	74080	162,0	859,6	65390	141,1	750,0

Analogous calculations of the utilized food and energy quantities can be given for the open Black Sea waters. During the first days of September, 1960, the expedition ship 'Akademik A. Kovalevsky' made a many-day station in the central part of the western sea region with quite insignificant currents; it was studying phyto- and zooplankton along with environment factors. Table 6 presents the average numerical magnitudes of Cladocera populations in that part of the sea, together with food quantities utilized by them within 24 hours. In order to approximately estimate the part which Cladocera appropriate out of the food and energy available in the sea, the general seston quantity suspended in the waters of the the western half of the Black Sea was calculated. The total quantity of organic matter (animate and inanimate) averages in this part 16 g of dry matter for 1 m^2 below the 0 - 20 m layer. Data, giving the composition of the animate organic (76)

matter and the relation of its magnitude to the detritus quantity in the surface waters of the Black Sea at the beginning of September, 1960, are presented on table 7.

Table 6

24-hour food and energy utilization by Cladocera populations in September, 1960, in the open waters of the Black Sea (below 1 m^2 of the 0 - 20 m layer)

(под 1 $м^2$ слоя 0 - 20 м)

Вид	number of ind. Численность, экз	Food consumption Потребление пищи mg dry m. мг сухого вещества	ashless mg Мг беззольного вещества	Kcal Ккал
Penilia avirostris				
Молодь young	10030	4,71	3,03	20,060
Взрослые adult	13300	46,60	20,97	247,380
Evadne spinifera				
Молодь young	70	0,02	0,01	0,084
Взрослые adult	510	0,98	0,74	5,508
Evadne tergestina				
Молодь young	550	0,11	0,09	0,660
Взрослые adult	4000	7,72	5,84	43,200
Итого Total	28460	60,17	39,68	316,892

The biomass of tow-net zooplankton and phytoplankton, collected with Nansen bathometers, was obtained from treated zoo- and phytoplankton samples by the workers of the plankton division of the Biology Institute of Southern Seas - T.M. Kondrat'eva and S.G. Kolosova. Data about the general quantities of micro-organisms in this region are taken from the writings of Y.I. Sorokin (1964). The detritus is calculated by the seston difference determined by Z.Z. Finenko (1965) for the western ~~halistase~~ region (defined by salt content?) by filtering water taken with bathometers, to which are added the quantities of phytoplankton and micro-organisms (15 700 mg - (107 + 80 mg)). The dry

T a b l e 7

Composition and quantity of the seston in the central part of the Black Sea below 1 m² of the 0- 20 m layer in September, 1960

Таблица 7

Состав и количество сестона в центральной части Черного моря под 1 м² слоя 0–20 м в сентябре 1960 г.

Kind of food / Вид пищи		Dry weight mg / Сухой вес, мг			
		raw weight / Сырой вес, мг	with ash / с золой	without ash / беззольный	Kcal / ккал
Zoopl.	Зоопланктон	2496	449	393	2,00
Phytopl.	Фитопланктон	531	107	53	0,27
Bacteria	Бактерии	400	80	73	0,37
Detritus	Детрит	—	15513	11446	58,37
	Итого / Total	—	16149	11965	61,01

weight of zooplankton is assumed to be 18% of raw weight, and that of bacteria and phytoplankton - 20%. Average ash content of zooplankton was = 12,6% of dry matter in 1960, according to data of Z.A. Vinogradova and others (1962). As to phytoplankton, ash content was calculated for individual taxonomic groups: Dinoflagellata - 29,0, Diatomea and Silicoflagellata - 57,3, colorless ciliated algae - 20,0 (Lanskaya, Pshenina, 1961), Coccolithophoridae - 53,8% of dry weight (Lanskaya, Vityuk, Rozhanskaya, 1964). Ash content in microorganisms was assumed to be = 9,0% (Werkman, Wilson, 1954). The tiny detritus particles (up to 10 μ) floating freely in the surface layer of 0 to 20 m, most probably, consists in the main of minute dead phytoplankton which is capable of decomposing quickly to sizes from 1 to 10 μ; the ash content of this detritus part was supposed to be = 20%, analogous to the ash content of minute cilia-moving algae. Ash content in

in detritus of sizes 10 - 350 μ was 36% (Skopintsev, 1947). For computing the caloricity it is supposed that 1 g ashless matter of plankton is equivalent to 5,1 kcal (Winberg, 1960).

In addition to the above, determining the amount of food which might be utilized by Cladocera populations was attempted for the same region. According to data of laboratory experiments, P. avirostris consumes algae up to sizes 8 μ and small detritus of the same size (Pavlova, 1959). From materials by T.M. Kondrat'eva, the general quantity of algae up to sizes 8 μ was computed. Data about the micro-organism biomass were taken from the writings of Y.I. Sorokin (1964). As far as correlations of detritus particles of various sizes are concerned, the only data available are for the Indian Ocean (Mullin, 1965). On the assumption that the correlation of minute and larger seston in the Black Sea is equal to the one of the Indian Ocean, detritus particles of size 1 - 10 μ would represent 58%, those of 10 - 350 μ - 39% of the general quantity of organic carbon suspended in the 20 m top layer. Assuming that organic matter contains 50% C, its total quantity (excluding zooplankton) below 1 m^2 of the 0 - 20 m layer in the central part of the Black Sea may be expressed by the magnitude of 5224 mg C. Estimating the available food for Cladocera, one can presume that 58% of all the carbon will serve to feed Penilia populations. (78)

Owing to the peculiarities of their mouth appendages, species of the genus Evadne seem to belong to the predators.

We inspected the intestine contents of two species - E. spinifera and E. tergestina - from among the material collected at the many-day station in 1963 and at the same point of the sea where it was done in 1960. In 40 inspected digestive tracts only 8 contained food. No vegetative food could be detected in these remains; the food lump regularly revealed small particles, transparent and non-transparent, very much like chitin, and the rest was an amorphous, structureless mass. As this mass could in no way be attributed to remains of vegetative origin, one can assume with a certain degree of certainty that Evadne's essential food consists of zooplankton and detritus. For the calculations it was accepted that all zooplankton organisms, smaller than 0,4 mm (Evadne's average body size) - eggs, nauplius and copepodid stages of Copepoda, Tintinnoinea - may consitute Evadne's food; as to the detritus, from among its general quantity they could utilize the medium-size particles - 10 to 350 μ (Mullin, 1965), which represents 39% of the overall quantity of carbon contained in particles from 1 - 500 μ (table 8).

T a b l e 8

Composition and quantity of Cladocera populations' food in the central part of the western half of the of the Black Sea in Sept., 1960, below 1 m² of the top 20 m.

Kind of food Вид пищи all in mg	*Penilia*			*Evadne*		
	dry Сухое вещество, мг m.	dry Сухое беззольное вещество, мг ashless	ккал kcal	dry Сухое вещество, мг	ash- Беззольное вещество, мг less	ккал kcal
Phytop. Фитопланктон	27	13	0,07	—	—	—
Bact. Бактерии	80	73	0,37	—	—	—
Zoop. Зоопланктон	—	—	—	63	53	0,30
Detr. Детрит	8975	7180	36,62	6028	3858	19,67
Итого Total	9082	7266	37,06	6091	3911	19,97

Thus, in 1960, the general quantity of dry organic matter in the open sea, apt to constitute the food of Cladocera polulations, is expressed by 15,173 mg or 57,03 kcal, which is 93% of all the seston in the 0 - 20 m layer. However, utilized were all in all by all the populations within 24 hours only 60 mg of dry matter, i.e., 0,4% of the matter suitable as food.

It seems interesting, just for the sake of information, to calculate that part of the general potential production of organisms, utilized as food by Cladocera populations. (79) It appears that such a calculation is possible on the basis of data gathered in 24-hour observations at sea in 1960 and from some sources of the literature. The production estimate for bacteria was based on the average 24-hour P/B coefficient equal to 0,7 which, in its turn, equals the mean of two magnitudes, adduced in the work of A.E. Kriss (1959); there is reason to believe, however, that this magnitude is too low. The production of phytoplankton organisms is determined from the rate of algal division in cultures (Mikhailova, Lanskaya, 1960; Lanskaya, 1961, 1965). The biomass accretion of naupliae and of copepodid stages of Copepoda, sizes up to 0,4 mm, was calculated according to the numerical quantities of these forms on three 24-hour stations on the basis of the period-lengths for every stage from data obtained by L.I. Sazhina (1960), and by the weight increase from stage to stage. The hypothesis was that naupliae and copepodids of Copepoda have a regular weight accretion with every stage; and it was

assumed that minute Tintinnoinea double their weight within 24 hours. To determine the chenges in detritus quantities within 24 hours was, unfortunately, not feasible. Results of the daily production evaluation of forms consumed by Cladocera below 1 m^2 of the 0 - 20 m open-sea layer in September, 1960, are given in table 9.

T a b l e 9

24-hour production of organisms utilized by Cladocera (below 1 m^2 of the 0 - 20 layer of the open waters of the Black Sea, in September, 1960)

Kind of food Вид пищи	raw w. Сырой вес, мг mg	dry w. Сухой вес, мг	ashless Беззольное вещество, мг m.	kcal ккал
Phytop. Фитопланктон размером to до 8 μ	341	53	28	0,14
Bact. Бактерии	280	56	51	0,26
Zoop. Зоопланктон размером to до 0,4 мм	90	16	14	0,08
Итого Total	711	125	93	0,48

Evaluations of the food quantities consumed by Cladocera populations in the north-western regions of the Black Sea were also carried out, and the available quantity of micro-organisms, calculated from data for August, 1951, was 40 mg within 1 m^3 of the 0 - 10 m layer (Lebedeva, 1957). It was assumed that the distribution of bacteria in the layer from 0 - 20 m was just as regular as from 0 - 10 m. Data concerning phytoplankton quantities were taken from materials of bathometer samples (for 1957) treated by co-workers of the (80)
phytoplankton laboratory at the Biology Institute of Soutern Seas. These samples were taken at the same stations where

numerical quantities and the biomass of Cladocera were computed (see table 1). The available quantity of zooplankton organisms was calculated from the data of L.I.Sazhina (1964) as being 8,3 g of raw weight below 1 m^2 of the 0 - 20 m layer. Since there were no data for the detritus, it was estimated to be the same as in the central regions, although it would seem reasonable to assume that in reality the relatively shallow north-western waters with all the river drainage ought to contain at least three times more inanimate organic matter than the open sea. Based on all this information, the general seston quantity floating freely in the nort-western part in the Black Sea in August, 1957, was calculated to be 17,427 mg of dry matter.

T a b l e 10

Food quantities for Cladocera populations in the north-western part of the Black Sea in August, 1957 (below 1 m of the layer 0 - 20 m)

Kind of food / Вид пищи	*Penilia* dry matter Сухое вещество, мг mg	*Penilia* ashless m Беззольное вещество, мг mg	*Penilia* kcal ккал	*Evadne* dry m. Сухое вещество, мг mg	*Evadne* ashless m Беззольное вещество, мг mg	*Evadne* kcal ккал
Phytopl. Фитопланктон	16	8	0,04	—	—	—
Bacteria Бактерии	160	146	0,74	—	—	—
Detritus Детрит	8975	7180	36,62	6028	3858	19,67
Zoopl. Зоопланктон	—	—	—	66	56	0,29
Итого Total	9151	7334	37,40	6094	3914	19,96

The useable food for Cladocera populations was evaluated only for Penilia and Evadne, since, the same as in 1957, the Podon population was very small in the north-western part of the sea (see table 10). The daily food quantity utilized by Cladocera in the north-western part of the Black Sea in

August, 1957 (see table 5) represented 1,5% of the general quantity of available food. Table 11 gives a picture of the 24-hour food utilization by all Cladocera populations in the Black Sea on a percentage basis in relation to the available food.

T a b l e 11

24-hour food utilization by Cladocera populations in the Black Sea (in %)

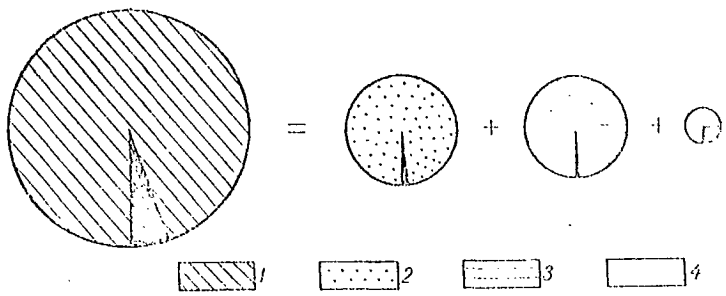
Суточное потребление пищи популяциями кладоцер в Черном море (в %)

Desig.of magnitudes Наименование величины, принятой за 100 % assumed to be 100%	North-west. Сеиро-западный район region		Central Центральный район region		
	dry Сухое вещество matter	кал cal	dry Сухое вещество matter	кал cal	
Весь сестон	1,3	2,1	0,4	0,5	total seston
Живая часть сестона (планктон)	0,4	0,4	0,8	0,9	animate " (plankton)
Потребляемые объекты:	1,5	2,5	0,4	0,6	Objects:
водоросли размером до 8 μ	3,5	9,7	1,0	1,5	algae to 8 μ
бактерии	2,2	2,1	0,6	0,6	bacteria
зоопланктон размером до 0,4 мм	9,8	10,0	7,0	6,3	zooplankton to 0,4 mm
детрит размером 1--350 μ	1,4	1,6	0,3	0,4	detritus 1 - 350 μ

In order to evaluate the quantity of utilized matter for each of the nutritive components in Cladocera rations (algae, bacteria, zooplankton, and detritus), it was necessary to adopt a few assumptions. There are no data about the ~~procentual~~ percentage ratios correlations of nutritive components for Penilia rations, but it is known that the crustacean indiscriminately filters all particles smaller than 8 μ (Pavlova, 1959). Therefore, the component ~~correlation~~ ratio in the ration was supposed to be analogous to the ~~correlation~~ ratio of food components in the sea (81) at the time when observations for Cladocera were recorded. For

Evadne it was assumed that the quantity of utilized detritus was equal to the consumed animate food. Cladocera juveniles eat bacteria and minute detritus particles. It is presupposed that the ~~correlation~~ ratio of these components in the daily ration for the young was equal to 50% of available bacteria quantities and 50% detritus up to 10 μ. Under these circumstances, the daily rations in the north-western part of the Black Sea in 1957, below 1 m^2 of the 0 - 20 m layer should be the following: 0,33 mg (1,7%) bacterial and 19,37 mg detritus food for young Cladocera; 0,3% algae, 1,7% bacteria and 98% of small detritus (0,57, 3,23, and 184,9 mg respectively of dry matter) - for adult Penilia. Adult individuals of the Evadne population utilized within 24 hours 6,5 mg zooplankton and 6,5 mg detritus. In the central region of the sea, in September, 1960, below 1 m^2 of the 0 - 20 m layer, juvenile Cladocera consumed 0,05 mg bacteria and 4,83 mg of detritus. Adult Penilia utilised 0,6% algae (0,28 mg of dry weight), 0,9% bacteria (0,42 mg) and 85% detritus (45,9 mg); adult Evadne - each 4,35 mg zooplankton and detritus. Such a correlation of nutritive components was used for the drawing and for the evaluations of table 11. These data (of table 11 and of the drawing) permit ~~to~~ the conclusion that in the Black Sea the significance of Cladocera as consumers of organic matter is not of great consequence. In the north-western regions of the sea Cladocera populations are much more numerous than in the open waters, which makes the role they play in the general balance of matter and energy

to be relatively more ~~considerable~~ important. It should be noted that Cladocera populations satisfy their nutritive requirements mainly by the organic matter contained in detritus and, therefore, the animate component of seston, utilized by Cladocera populations, is quite insignificant (0,4 - 1,5%). At the evaluation of the food quantity utilized by Cladocera (in addition to detritus) on a percentage basis for the daily production of all consumed forms in the central part of the Black Sea, it turned out that Cladocera populations eat 0,5% of the up-to-8-μ algae production, 0,8% of the bacteria production, and 27% of the minute zooplankton organism production. The overall quantity of the ration part consisting of animate objects, constitutes 4% of the 24-hour production of these organisms (see drawing). (82)



Суточное потребление сухого органического вещества (в % от потенциальной продукции) популяциями Cladocera в центральной части Черного моря в 1960 г. (черные сектора): *1* - общая суточная продукция организмов, потребляемых кладоцерами, *2* - продукция бактерий, *3* — продукция водорослей размером до 8μ, *4* — продукция зоопланктона размером до 0,4 мм.

24-hour utilization of dry organic matter (in % of potential production) by Cladocera populations in the central part of the Black Sea in 1960 (four sectors). 1 - the general 24-hour production of organisms consumed by Cladocera; 2 - production of bacteria; 3 - production of algae up to 8 μ; 4 - production of zooplankton up to sizes 0,4mm.

In September, 1960, Oikopleura dioica, copepodids of Paracalanus parvus and Acartia clausi were feeding competitors of Cladocera young and grown Penilia in the epiplankton complex of the open sea; and along with these - all nauplıar stages of Copepoda which began to feed, the smaller copepodid stages of all other epiplankton Copepoda, and to a certain degree - mollusc larvae. If we tentatively assume that the ration of these organisms averages 50% of their body weight, then the entire quantity at hand will consume 406 mg of dry matter within 24 hours. And the over-all utilization of nutritive substances ~~substances~~ up to the size of 8 to 10 μ (including detritus) by all the organisms of the epiplankton complex will be expressed by a magnitude representing 3% of the quantity of nutritive substances available in the sea. These rough estimates permit to assume that in the Black Sea the Cladocera populations are abundantly provided with food, and that their considerable nutritive requirements can be fully satisfied. As we already mentioned, these are essentially met by the inanimate seston. According to the data of Z.Z. Finenko (1965), the quantity of inanimate seston is many times greater than its animate portion (85 - 95% of all the organic matter floating suspended in the water). It is most probable that this per- (83)
centage quantity comprises some plankton in addition to the inanimate part, namely the organisms which cannot be collected by zooplankton tow-net methods and, possibly, great quantities of ultra-nannophytoplankton which is being destroyed at fixation.

In this case, the quantity of living matter in the Cladocera ration might be somewhat greater, but this will not alter the over-all picture of Cladocera's nutritive requirements being fully assured in the Black Sea.

Conclusions

In the summer, Cladocera populations represent one of the preponderant components (both in numbers and in biosmass) of the epiplankton community in the Black Sea.

By the method of closed glass containers placed on fixed ~~water levels~~ depths in the sea, the intensity magnitudes of oxygen utilization for three ~~massive~~ important Black-Sea Cladocera species were determined. At 20° C, adult females of Penilia avirostris expended on energetic metabolism 0,065, juveniles - 0,011, Podon polyphaemoides - 0,012, Evadne spinifera - 0,054 mg O_2 per hour for 100 individuals, or correspondingly 6,2, 0,7, 1,2, and 5,3 cal in 24 hours.

Based on the quantities of oxygen utilization and the weight accretion in body mass of Cladocera, their probable nutritive rations were evaluated. At the periods of their ~~massive~~ mass development, the daily rations of Cladocera populations are the following: P. avirostris - 73, P. polyphaemoides - 71, E. spinifera - 120% of body weight.

Owing to the rapid weight increase and parthenogenetic reproduction, the average expenditure for ~~plastic~~ growth matabolism represents up to 50% of the physiologically utilizable food.

The coefficient of food utilization for growth (K_2)

for females of all three species in the growing period, was equal to 0,25 - 0,26, for Penilia young - 0,53. Of the over-all quantity of physiologically useful food, juvenile broods utilize for weight increment 54,2%, adult growing females - up to 20%.

An attempt was made to estimate the part of Cladocera populations in the general matter-and-energy balance of the Black Sea. It appears that they consume up to 2,0% of all the available seston mass, and up to 0,8% of its animate component in relation to dry matter.

In September, 1960, the following calculations were arrived at in the open waters: the general seston quantity below 1 m^2 of the 0 - 20 m layer (16,149 mg of dry matter), the food quantity for Cladocera populations (15,173 mg of dry matter), and the magnitude of the potential 24-hour production of animate plankton forms consumed by Cladocera (125 mg of dry matter). The quantity of dry organic matter utilized by Cladocera populations in that region consituted 0,4% of the first above quantity, 0,4% of the second, and 4,0% of the third quantity.

In the north-western region of the sea, which is (84)
characterized both by the greatest numbers and the largest biomass of Cladocera populations, these consume within 24 hours up to 1,5% of the available quantity of all utilizable nutritive substances. The part of algae up to size 8 μ, consumed by Cladocera, represents 3,5% of all the mass available

in the sea, of bacteria - 2,2%, and of detritus - 1,4%.

This entitles us to conclude that in the Black Sea Cladocera are obviously well provided with food, and their considerable daily rations are essentially met by the organic detritus matter.

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