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THE NUTRITIVE VALUE OF THE DETRITUS FOR THE MARINE PLANKTON ANIMALS

VALEUR NUTRITIVE DES DETRITUS POUR LES ESPECES ANIMALES PLANCTONIQUES MARINES

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The detritus follows the DOM as the second biggest oceanic energy accumulating resource which is comparatively slow to find the possible way to the biotic cycle. According to the U-shaped Odum pattern of energy flows, the detritus food chain is a major channel of both matter and energy transformation in sea- and freshwater reservoirs.

The earlier quantitative data on detritus in different regions of the World Ocean show that it averages 80 to 90 % total organic suspension in the open seas and oceans and 50 to 90 % in the coastal areas (Finenko, Ostapenya, 1971 ; Finenko, Zaika, 1970). The research initiated by the South Seas Biology Institute in the early'60s showed that detritus amounts to 90 % total organic suspension in the Black, Mediterranean and Arabian Seas, as well as in the tropical zones of the Pacific and Atlantic Oceans. The initial calculation of the amount of the detritus as a difference between the total suspension and sum of the phyto-, zoo-, and bacterioplankton overpredicted the value of the suspended dead fraction which might be caused by the imperfect plankton collection techniques. The introduction of the advanced ATP living- fractions-determination techniques and simultaneous measuring probes permitted to increase the accuracy of the dead organic matter quantification which supported in principle the right conclusion that detritus is an important structural element of the ecosystem (Tabl.1). The detailed studies showed the irregular vertical distribution of detritus and considerable seasonal quantitative variations (Manuels and Postma, 1974 ; Poulet, 1976 ; Lenz, 1977).

In the reservoir the dead organic matter undergoes rather complicated biological and physico-chemical transformations with microbial transformation playing the major part. The very massive presence of bacteria here should be considered as the most important index of the nutritive value of detritus. According to Odum, detritus consists of the particulate dead organic matter and relevant microflora.

However, the number of bacteria on the detritus particles appeared to be quite variable and not so high which fact led certain authors to sceptical conclusions about the nutritive value of detritus. Wiebe and Pomeroy (1972) showed that only single bacteria stuck to the detritus particles in subtropical and antartic water, coral reefs and estuaries (after Ostapenya, 1975). 80 % and more bacteria do not aggregate and do not stick to the detritus particles.

Still smaller amount of bacteria (about 4 % total) was found stuck to the detritus particles in Kilsk Bay, Baltic Sea (Zimmerman, 1975). I.A. Melnikov (1974) found insignificant number of microorganisms on the oceanic detritus coarse fractions, while Pearl (1973) found the same on the detritus particles in the upper layer of the water column in Takhoë Lake.

However, one should note that in the case of the stuck bacteria their biomass percentage may somewhat exceed the percentage of their number because on the detritus particles coarser rod-like bacteria tend to prevail while cocci dominate in suspension (Fergüsson and Rublee, 1976). In the fore-going part we related the amount of bacteria stuck to the detritus particles to their total. The estimated mass of bacteria is about 5 to 50 % mass of the detritus particles with maximum probability value of 10 % (Ostapeny, 1979). Thus bacteria mass/mass of the particles ratio may be rather high.

The great amount of the suspended detritus and insignificant relative content of the living fraction, which cannot always provide for the nutrition of the aquatic zooplankton under different trophic conditions, lead scientists to conclude that zooplankton can and should use detritus for nutrition. The majority of the authors makes this conclusion on the basis of indirect data, e.g. chemical composition. The high protein-carbohydrate content as well as the presence of aminoacids, making up to 60 % total protein, is an important argument in favor of such conclusion (Parsons, Strickland, 1962 ; Melnikov, 1974). The size of the detritus particles follows the chemical composition as a major indicator of the possible feeding of the plankton animals on detritus. Their dimensions vary within the wide range : from finely dispersed particles (under 1 μ) to coarsely dipersed aggregated ones (up to 200-500 μ). It has been shown that under different trophic conditions in ocean the coarsely dispersed fraction (10 to 200 μ), i.e. the particles susceptible to filtration from water by mesoplankton, make up only 15 to 50 % total organic carbon in the suspension. Thus only half of the total detritus can be uses by the zooplankton filtrators, i.e. the part of the potential detritus food is not so great as it was earlier assumed (Melnikov, 1974).

The great amounts of the detritus particles were found in the intestines of the animals and this is another indirect proof of detritus consumption by plankton animals. Flurorescent microscopy helped to find that contents of the front part of the intestines in Calanoida *Undinula vulgaris* in the Eniwetock Atoll Lake included 95 % detritus and only 2 % intestines' material fluoresced as chlorophyll. The considerable amount of detritus was found in the intestines of *Oikopleura longicauda* larvae and adult *Acartia tonsa* in the Narragasett Bay (Gerver and Marshall, 1974).

By now there have been only scarce observations and experiments on detritus consumption by the marine plankton animals. Interesting results were obtained by Poulet (1976) who had been studying annual consumption of both living and dead particles in plankton by *Pseudocalanus minutus* in the Bedford Bay. Having compared total carbon and ATP content in supension he demonstrated that detritus is the most important nutriment in the annual rations of animals ; despite the season the Copepoda consumed more dead carbon than living one. The dead and living carbon in their nutriment averaged 71 and 29 % correspondingly. In our experiments with another species of *Pseudocalanus* (*P. elongatus* from the Sevastopol Bay) crustaceans also consumed detritus of the single-celled algae in amounts comparable to the living algae (27 and 14 % body mass daily correspondingly) (Pavlovskaya, Pechen-Finenko, 1975). Similar results were obtained in certain orders of oceanic Copepoda in the western part of the South Atlantic anticyclon circulation (*Calanus minor, Pleuromamma gracilis, Undinula vulgaris*) (Pavloskaya, Kosikhina, 1979). When the mixture of living algae and fresh detritus from the Dinoflagellata was offered to the animals as a nutriment in the short-term experiments, the consumption of both types of nutriment was practically equal and made up daily 5.0.27.0 % body mass. Other species can also consume fresh vegetal detritus (from both micro- and macroalgae) in amounts comparable to the algae : *Calanus helgolandicus* (Paffenhöfer, Strickland, 1970 ; Heerkloss, 1980), *Acartia tonsa* (Roman, 1977), *Undinula darwini* (Petipa *et al.*, 1974 a, b). The animals not only consumed detritus, but included the consummed matter into their body tissue. The relative efficiency of incorporation in *A. tonsa* varied from 10 to 45 % consumed detritus and from 18 to 55 % algae *Nitzchia closterium* depending upon the nutriment concentration (Roman, 1977).

However, there are also data in literature contradicting the foregoing demonstrations of the plankton animals abilities to consume considerable amounts of detritus. Relative incorporation rate of phyto- and zoogenous detritus, i.e. incorporated carbon/carbon-in-the-body content ratio in Mysid *Neomysis mirabilis* (Possiet Bay, Sea of Japan) and freshwater *Diaptomus graciloides*, was by an order smaller than in living algae (Pechen-Finenko, Pavloskaya, 1975 ; Pechen-Finenko *et al.*, 1975) (Table 2).

The intensity of feeding in *Calanus*, measured by the fecal pellets excretion per time unit, was ten times lower with the dead suspension consumption than with the living algae consumption (Corner *et al.*, 1974). The animals failed to maintain the initial level of nitrogen and phosphorus in their body loosing them as the starving animals did which proves that population cannot survive for a long period feeding on the dead suspension.

With only few exceptions the foregoing experimental data were obtained on monotype nutriment ; they do not represent the importance of the consumption of detritus in suspension with fresh food under free-choice conditions. This constraint is removed by the studies performed by T.V. Pavlovskaya *et al.* (Pavlovskaya, 1979 ; Pavloskaya, Abolmasova, 1981 ; Pavlovskaya *et al.*, 1975) on large variety of copepods from different regions of Atlantic and Indian Oceans in which different nutriments consumption rate under free-choice conditions was measured with the help of carbon-14 balance in short-term experiments. They demonstrated that all studied species consumed very small amounts of detritus ; the animal nutriment was the main consumed component of the nutrient suspension. The typique consumption of components is shown in table 3.

Even in the case of the low consumption of detritus the effectiveness of its incorporation is comparable with that for algae. The short-term experiments show 84 % incorporation of the detritus of single-celled algae by mysid *Neomysis mirabilis* and 50 to 70 % incorporation of three kinds of phytogenous detritus by *Pseudocalanus*. All studied species of the oceanic zooplankton showed 40 to 80 % assimilation of detritus ; this value is in close proximity to that of algae assimilation (Pavlovskaya *et al.*, 1975). The incorporation of detritus may depend on its age. Really, the experiments with the freshwater zooplankton demonstrated the inverse relationship between the age of detritus and its susceptibility to assimilation : maximum assimilation effectiveness was observed one-day detritus (75 %), 4-27 day detritus showed 60 % assimilation ; the assimilation dropped with the aging of detritus and amounted only to 14 % after 40 days of decomposition (Pavlovskaya, Ostapenya, 1976 ; Pavlyutin, 1979).

The above data were obtained in the short-term experiments : feeding time varied from hours to minutes. These experiments are useful in evaluation of consumption rate for detritus, especially, in comparative studies, as well as assimilation of detritus, at the same time they are insufficient to estimate nutritive value of detritus which could be established only in the long-term experiments. Unfortunately, such experiments on marine plankton animals are rather scarce, may be due to the lack of established procedures of long-term cultivation of crustaceans in the laboratory experiments.

In the long-term experiments with *Acartia tonsa* fed by detritus from the desiccated *Fucus vesiculosus* plants, the animals stopped to grow, and toward the end of day 10, the author observe 100 % death of the crustaceans, similar to that of the starving animals (Roman, 1977). Estuarine copepods *Eutrytemora affinis* and *Scottolana canadensis* survived better on detritus from the swamp plants : survival was 20 to 90 % on day 20 depending on the kind and concentration of detritus (Heinle *et al.*, 1977). The detritus-fed animals produced eggs and nauplii, but their number was much lower than in the case of algal or mixed detrital and algal nutriment (Table 4).

These data do not permit us to highly estimate the nutritive value of detritus for marine plankton copepods, though one cannot fail to see its importance as a supplementary nutriment, especially for the estuarine species.

The above data concerned the nutritive value of the detritus from the dead single- and multicellular algae. As a rule, there was fresh detritus after 1-4 day decomposition, in experiments. It is shown that maximum growth of bacteria is observed on the artificial detritus particles during the first 1 to 3 days (Pavlyutin, 1974 ; Heinle *et al.*, 1977). The same is true for the natural detritus. If we assume that the nutritive value of the detritus is determined primarily by microbiota, we may expect the maximum potential nutritive value of these particles in the first place. Indeed, plankton Copepoda use practically no organic matter of the "aged" detritus or humus (Petipa *et al.*, 1974a, Pechen- Finenko, Pavlovskaya, 1975).

Another kind of dead component of the suspension (aggregates produced by the DOM sorbtion on the surface of phase separation) can be consumed by Artemia salina (Baylor, Sutcliffe, 1963) and freshwater Cladocera (Kuznetsova *et al.*, 1984). But neither growth effectiveness of *Artemia*, nor fertility of *Simocephalus* reached considerable values as compared with the living food. *Calanus helgolandicus* consumed no natural aggregates in experiment though it ate phytogenous detritus and feces (Paffenhöfer, Strickland, 1970). Ther is no apparent proof of the high trophic value of aggregates for the plankton animals.

Thus far there is no positive solution to the problem of the nutritive value of detritus for the aquatic and, first of all, marine plankton crustaceans. No doubt, they can consume certain amount of the fresh detritus, but it is not a nutriment of full value ; there is no proof that detritus can supply energy needed for the animals during any considerable time. It may eventually play the part of supplementary, though not exclusive, source of nutriment during certain periods of the annual succession of the plankton community.

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Reservoir	Depth, m		% total suspension: phyto-plankton	hetero-trophs	detritus	Author
Black Sea	euphotic zone		0.2-1.0	5.4-20.0	78-95	Finenko, Zaika, 1970
Sea of Azov	-"-		5 -10	3.3-17.0	80-92	-"-
Atlantic Ocean						
- along the 15th meridian	-"-		0.5-1.3	0.6*	98-99	-"-
- along the 16th parallel	-"-		0.6-1.7	0.7*	98-99	-"-
Pacific Ocean	0-100				63	Finenko, Ostapenya, 1971
Kilsk Bay, Baltic Sea	mixed layer		26.7	32.7	40.6	Lenz, 1977
	lower layer		22.8	34.6	42.6	-"-
Bedford Bay, Atlantic Ocean	5		7.41		62-93	Poulet, 1976
Atlantic Ocean southern anticyclonic circulation	0-100	1	12.4	11.0**	76.5	Vityuk, 1983
		2	0.8	4.8**	94.3	
		3	0.3	3.1**	96.6	

*w/o bacteria

**w/o zooplankton

TABLE I - DETRITUS AS STRUCTURAL ELEMENT OF THE ECOSYSTEMS

Species of the animal	t°	Nutriment	The hourly 'accumulation index', %	Source
Neomysis mirabilis Possiet Bay, Sea of Japan	18-20	Vegetal detritus (Platymonas + Cladophora)	$1.9 \cdot 10^{-2}$	Pechen-Finenko, Pavlovskaya, 1975
		Animal detritus (Gammarus)	$5.4 \cdot 10^{-2}$	
		melanin	$3.0 \cdot 10^{-3}$	
		G.kowalevskii	$3.4 \cdot 10^{-1}$	
Diaptomus graciloides (Naroch Lake)		Animal detritus	$1.7 \cdot 10^{-2}$	Pechen-Finenko, et al., 1975
		Vegetal detritus		
		duckweed	$1.7 \cdot 10^{-2}$	
		elodea	$1.0 \cdot 10^{-2}$	
		Chlorella vulgaris	$6.0 \cdot 10^{-1}$	
		Staurastrum	$5.1 \cdot 10^{-1}$	
		Scenedesmus	$2.8 \cdot 10^{-1}$	
		Tabellaria	$1.1 \cdot 10^{-1}$	
		Diatoma	$9.1 \cdot 10^{-2}$	
		Ankistrodesmus	$4.1 \cdot 10^{-2}$	
		Bacteria	$1.0 \cdot 10^{-2}$	

TABLE II - THE HOURLY "ACCUMULATION INDEX" VALUE IN PLANKTON CRUSTACEANS DEPENDING UPON THE CONSUMPTION OF DIFFERENT NUTRIMENTS

Species of animals	t°	Type of nutriment	Ration,% body mass	Incorporation,%	Author
Scolecithrix danae	21	Vegetal detritus	1.4	57.0	Pavlovskaya, Abolmasova,1981
		Gymnodinium lanskaya	0.4	50.0	
		small copepods	13.2	41.7	
Pleuromamma abdominalis	-"-	Detritus	3.7	56.6	-"-
		Gymnodinium	0.4	50.0	
		small copepods	57.3	55.0	
Euchaeta marina	-"-	Detritus	0.5	60.0	Pavlovskaya et al.,1975
		Gymnodinium lanskaya	6.0	91.8	
		Onceae	59.0	51.0	

TABLE III - DIFFERENT TYPES OF NUTRIMENT : RATIONS AND EFFECTIVENESS OF THEIR ASSIMILATION BY PLANKTON CRUSTACEANS

	Algae $3.75 \cdot 10^4$ cells/ml	Detritus $25 mg \cdot l^{-1}$	Detritus + algae	Sea water, filtered through 0.45μ filter
Average number of eggs per chamber	14.9	7.5	17.8	-
Production rate nauplii/ . day	1.8	0.7	3.5	-
% of 20 day survivals ♀♀	90.0	90.0	60.0	10.0

TABLE IV - FERTILITY AND NAUPLII PRODUCTION RATE IN SCOTTOLANA CANADENSIS DEPENDING ON THE TYPE OF NUTRIMENT (HEINLE ET AL., 1977)