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On the role of organic detritus in the pelagic food web

by

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Introduction

LOHMANN (1908) was one of the first planktologists to draw attention to detritus as a potential food resource for herbivores during the winter months in northern regions, when phytoplankton is scarce. Yet it took over half a century before an intensive investigation on the abundance and quality of detrital matter suspended in the sea was commenced. (KREY 1961, PARSONS a. STRICKLAND 1962, RILEY et al. 1964, NEMOTO a. ISHIKAWA 1969, GORDON 1970 and others).

This lapse of time may be explained not only by a general neglect of the detritus problem but also by the lack of suitable methods for its investigation. The methods have still to be improved, since even today the quantitative measurement of organic detritus is only indirectly possible. The usual procedure, the measurement of total particulate organic carbon followed by subtraction of phytoplankton carbon, which is calculated by means of cell counts, leaves unconsidered the carbon content in heterotrophic organisms such as microzooplankton, nonpigmented flagellates and bacteria.

Except for deep-sea samples, we can assume that a considerable portion of particulate carbon obtained by filtration of water samples originates from microzooplankton and heterotrophic microorganisms. For this reason the estimation of albumen (KREY et al. 1957) or ATP (HOLM-HANSEN a. BOOTH 1966, HOLM-HANSEN a. PEARL 1972), which occur in all organisms in more or less constant proportions, seems to be a more adequate method of separating planktic from detrital organic matter. However, even using such a correction to avoid an overestimation of organic detritus will probably not effect any basis change in the overall picture of the predominance of organic detritus over phytoplankton.

As stated by STEELE (1974), there is a controversy on the significance of organic detritus as part of the pelagic food web. While some investigators such as KREY (1961) and RILEY (1963) consider it an important food resource for pelagic filter feeders, other authors call for more reservation in discussing this hypothesis (STEELE 1965, JØRGENSEN 1966). The main argument against it is that the large standing stock of detritus usually observed seems to indicate a low utilisation by grazers.

But so far there is very little evidence that filter feeders such as copepods are capable of a qualitative food selection (JØRGENSEN 1966). In discussion the food value and significance of organic detritus we must therefore proceed from the basis assumption that phytoplankton and detrital matter are ingested by herbivores at all seasons in the proportion in which are present. The only valid criterion for selection seems to be that of particle size; food is selected according to the size of the feeders and the construction of their filter mechanisms. Thus viewed, data on the amount of organic detritus in a particle size group suitable for filter feeders are of interest.

Material and methods

The data reported are part of a comprehensive study on the amount and composition of total particulate matter-including zooplankton up to the size of about 1 cm-in the Western Baltic. Sampling was performed at several stations situated in the western part of the Kiel Bight; these were alternately visited at approximately four-week intervals during one year in 1970/71. Since a detailed description of sample taking and analytical methods has already been given in other papers (LENZ 1973, 1974), they will only be briefly described here.

A total of 114 large-volume water samples were taken from different depths by means of a vacuum-operated plankton pump (LENZ 1972) and fractionated into 4 size groups (1-150, 150-300, 300-600 and >600 µ). Since the bulk of particulate matter is mostly concentrated in the smallest size group-this was confirmed by the results (LENZ 1974)-the measurement of organic detritus was confined to this fraction. As pointed out already, the values were obtained indirectly by taking the difference between total organic carbon and plankton carbon including phytoplankton and heterotrophic organisms. The protein or albumen content measured by the method of KREY et al. (1957) was converted into carbon as follows: The average values 1 : 1.25 and 1 : 0.77 were chosen for the ratio protein to carbon in phytoplankton and in heterotrophs, corresponding to a percentage of protein in organic matter of 40 and 65 respectively. Organic matter is taken as twice the carbon content. All values given in this paper are expressed as dry organic matter in mg m^{-3}.

Results

Seasonal abundance

The concentration of organic detritus (1-150 µ) in discrete samples taken between the surface and the bottom of the water column varied from 30 to 840 mg m^{-3} with a rounded off mean value of 210 mg m^{-3} during the investigation period. This large variation is reduced to about the factor 6 when the values of each station are grouped into a mixed homogeneous surface layer and a variably stratified lower layer, following the main hydrographic structure of the Western Baltic.

Fig. 1 shows the seasonal variation for both these layers. The highest values are found during summer in May and September. The maximum for the lower layer in May corresponds to an extremely high phytoplankton and zooplankton standing stock comprising mainly the higher size classes. The high value in January in probably caused by sediment stirred up from the bottom as a strong current was observed during sampling.

What is interesting is that the lowest concentrations were observed in both layers in March and early April immediately after the phytoplankton spring bloom characteristic of this area for the first half of March. But surprisingly no pronounced bloom was observed in spring 1971 at the time of observation. It could not be subsequently established whether the missed bloom occurred during the 18-day interval between St. 14 and St. 15 or if the phytoplankton was prevented from developing a high standing crop through heavy zooplankton grazing in that year. A mild winter and a relatively high copepod population found as early as February favour the second explanation. The occurrence of a similiar situation in some years is reported for the spring bloom in Danish waters by STEEMANN NIELSEN (1963).

As indicated by fig. 1, about one to two thirds of the total organic matter in the size fraction 1-150 µ consists of detritus. Although some stations show an inverse ratio, the lower layers seem to contain a somewhat higher percentage of detritus. This accumulation can be ascribed to the sinking of phytoplankton fragments and faecal material. With the exception of May, the relative abundance of detritus appears to reach its maximum in winter. This is probably due to small sediment particles being frequently brought into suspension through strong winds during the process of vertical mixing in a shallow coastal area like the Western Baltic.

The following table shows the annual mean composition of total particulate matter in the size fraction 1 - 150 µ.

Tab. 1

	Mixed surface layer $mg\ m^{-3}$	Mixed surface layer %	Lower layers $mg\ m^{-3}$	Lower layers %
Phytoplankton	135	26.7	112	22.8
Heterotrophs	165	32.7	170	34.6
Detritus	205	40.6	210	42.6
Total	505	100.0	492	100.0

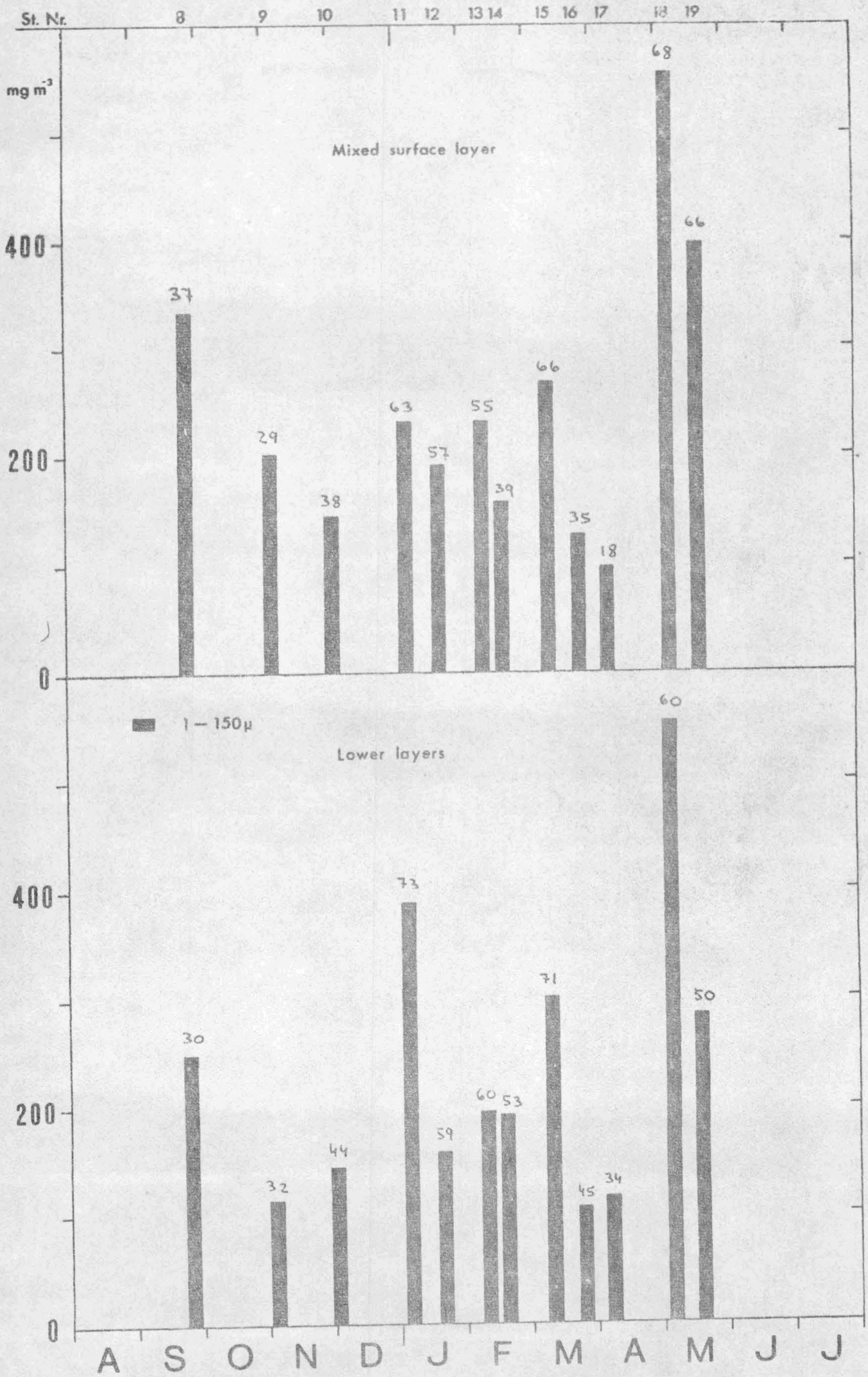

Fig. 1 Seasonal variation of organic detritus (1-150 µ) expressed as dry weight of organic matter. Figures above the bars indicate the percentage of detritus in total organic matter (1-150 µ).

That phytoplankton ranks behind heterotrophs here is explained by the composition of the latter in which four main groups can be distinguished as follows:

1) small herbivores (ciliates, holo- and meroplanktic larvae) belonging to microzooplankton

2) non-feeding organisms (here termed 'inactive') such as eggs, cysts and the first two naupliar stages of copepods

3) non-pigmented flagellates

4) bacteria, yeasts and fungi mostly associated with detritus particles

Groups 3 and 4 may be classified as heterotrophic microorganisms; together with group 2 they may be termed heterotrophic microplankton.

Only a very rough estimate can be given of the average standing stock of these four groups in our coastal area. It is assumed that groups 1 and 2 comprise about 25 % each and groups 3 and 4 together about 50 % of the heterotrophs in the size fraction 1 - 150 µ. When only the ratio of heterotrophic microorganisms to phytoplankton and detritus is considered, the order of the figures in tab. 1 is changed inasmuch as the heterotrophic microorganisms now amount to about 70 % of the phytoplankton and to about 40 % of the detritus standing stock, taking the average for both layers.

Yet these figures must be regarded as tentative. They cannot provide more than a vague idea of the mean ratios in particulate organic matter, which will obviously vary considerably with geographic, hydrographic and seasonal conditions.

Origin

When regarding the seasonal pattern of detritus, phytoplankton and heterotrophs, the presence of some sort of synchronisation is sought for, especially between detritus and the other components of particulate matter. Since some information on the origin of organic detritus in the pelagic environment may be thereby derived, the correlation coefficients for detritus to phytoplankton and to heterotrophs were calculated first for each station (tab. 2) and then for the upper and lower layers (tab. 3) by putting together all values according to their depths.

Looking at r in tab. 2 first, we find only four significant correlations. In September and November detritus is positively correlated with phytoplankton. This favours the interpretation that detritus mainly originated from phytoplankton in these cases. But the very contrary appears to be true in December, when the relative concentration of detrital matter suspended in the water column starts to increase (fig. 1). The only significant correlation between detritus and zooplankton - observed in May - is negative as well. When the multiple correlation (R) is applied, two of the four significant correlations are excluded.

Tab. 2 Correlation coefficients (simple (r) left, multiple (R) right) between organic detritus (1-150 µ) and the size fractions 1-150 µ und 1- 600 µ for the organic component in phytoplankton and heterotrophs respectively (* = 5 %, ** = 1 % significance level)

St.	Month	Phytoplankton		Heterotrophs		n - 2	Phytoplankton		Heterotrophs		n - 3
		1-150 µ	1->600 µ	1-150 µ	1->600 µ		1-150 µ	1->600 µ	1-150 µ	1->600 µ	
8	Sept.	0.9867*	0.9864*	0.8332	0.8972	2	0.9664	0.9679	0.4800	0.7383	1
9	Nov.	0.5598*	0.6146*	-0.0485	-0.1082	14	0.6467*	0.7305**	0.3933	-0.5091	13
10	Dez.	-0.5103*	-0.5238*	-0.3792	-0.3491	14	-0.4926	-0.4520	-0.3510	-0.1927	13
11	Jan.	-0.4456	0.4639	0.7483	0.3642	3	-0.0445	0.3308	0.6724	0.1257	2
12	Jan.	0.3303	0.3947	-0.1612	-0.0812	6	0.4406	0.4027	-0.3450	-0.1190	5
13	Feb.	0.0657	0.0230	0.3389	0.1614	5	0.1527	-0.1774	0.3692	0.2371	4
14	Feb.	-0.4721	-0.4325	-0.1842	-0.6634	5	-0.4919	-0.6092	-0.2402	-0.7529	4
15	March	-0.3543	-0.3277	0.2299	-0.1149	5	-0.2801	-0.5753	0.0430	-0.5126	4
16	March	-0.4845	-0.4219	0.1470	-0.0678	14	-0.5153	-0.445	0.2471	0.1686	13
17	April	-0.3080	-0.2678	-0.3226	-0.2233	9	-0.0011	-0.2028	-0.1009	0.1364	8
18	May	-0.7033	-0.0458	-0.6194	-0.2411	4	-0.5234	0.8501	-0.3385	-0.8584	3
19	May	0.0334	0.0334	-0.6171*	-0.7598**	9	0.1433	0.1170	-0.6267	-0.7633*	8

Tab. 3 Correlation coefficients (simple (r) right, multiple (R) left) between organic detritus (1-150 µ) and the size fractions 1-150 µ and 1->600 µ for the organic component in phytoplankton and heterotrophs respectively independent of season (* = 5 %, ** = 1 % significance level)

Layer	Phytoplankton		Heterotrophs		n - 2	Phytoplankton		Heterotrophs		n - 3
	1-150 µ	1->600 µ	1-150 µ	1->600 µ		1-150 µ	1->600 µ	1-150 µ	1->600 µ	
Upper	-0.1322	-0.0506	-0.1812	-0.0772	63	-0.0046	0.0028	-0.1251	-0.0584	62
Lower	<u>0.2982</u>*	<u>0.4485</u>**	0.2375	<u>0.3071</u>*	47	0.2000	<u>0.3617</u>*	0.0759	0.1208	46

The main feature of tab. 3 is the striking difference between the layers. No correlation between detritus and phytoplankton or zooplankton standing stock appears to exist in the mixed surface layer, which comprises the upper 10 - 15 metres. But the situation is altogether different in the lower layers, especially when the simple correlation (r) is taken into account. Detritus (1 - 150 μ) seems to be mainly correlated to total phytoplankton and in a lesser degree to total zooplankton. But again the significance of these correlations decreases in the corresponding multiple correlation coefficients.

Summarizing these observations, it is extremely difficult to draw any conclusions as to the origin of organic detritus. One obstacle is that the correlations calculated are probably biased by the fact that the three variables are not completely independent of each other because of the mthod of determination used. A second problem arises from the difficulty of combining the results found for both layers. While the concentrations of detritus are approximately the same in both layers (fig. 1 and tab. 1), its relation to phyto- and zooplankton differ so strongly. Decaying phytoplankton and faecal material originating chiefly from microzooplankton, which produce small pellets that mostly disintegrate before reaching the bottom, can be looked upon as the main producers of detritus in the lower layers. However,nothing conclusive can be said on the origin of detritus in the upper layers.

<u>Significance in the food web</u>

There are at least three aspects which are of importance in considering the value of detritus as food for filter-feeding herbivores. Let us start with particle size. The size spectrum of detritus seems to fit in with that suitable for filter-feeders. Size analyses (e.g. LENZ 1968, 1972) have shown that detrital matter is mainly concentrated in a size range from 1 to 55 u. Thus we can assume that the size fraction 1 - 150 u measured in our investigation comprises all detrital matter capable of being ingested by filter-feeders.

The second aspect deals with the nutritive value of detritus. The food value of a detritus particle is determined by the percentage and nutritive properties of the organic substances present in it. Both these depend on the origin and age of the particle as well as on environmental conditions. A particle with a very small portion of digestible organic matter will not have a significant food value when the energy gained through its ingestion is less or equal to the energy required for its intake and digestion.

The third aspect concerns the mechanisms by which the nutritive value of a detritus particle may be increased. The first process, the adsorption of dissolved organic matter by inorganic particulate matter, is of a physico-chemical nature. It provides to a large extent the foundation for the second process, a biological one, by making possible the existence of microorganisms assimilating the organic substances adsorbed. Microorganisms growing on detritus particles increase by their high protein content the nutritive value of the latter considerably. Not only do they greatly augment the nutritive value of organic substances, they also convert dissolved organic matter into particulate. These microbiological processes are doubtless of great importance in the marine food chain. By supplying a large surface area - this can easily reach dimensions of several m^2 per m^3 water (comp. LENZ 1968) - for bacteria to settle on, detritus particles support bacterial growth to a far-reaching extent.

In the above context a third process, also of a physico-chemical nature, as proposed by RILEY (1963, 1970) must be mentioned, although its significance in situ has not been established so far. This is the formation of larger organic particles through aggregation of smaller ones together with adsorption of dissolved organic substances. Thus very small particles not directly consumable by filter-feeders could reach a filterable size.

On reviewing what has been said of the nutritive value of detritus and the amount of its organic fraction measured - the biomass of bacteria etc. attached to it, being part of the category heterotrophs, is not included here -, it seems obvious that organic detritus must play an important role in the pelagic food web. At least for the euphotic zone and the immediately underlying layers we can assume that a large portion of detrital organic matter is of some nutritive value to filter-feeders. Organic detritus therefore constitutes an additional food source at all seasons besides phytoplankton, although its nutritive value is expected to vary considerably in relation to phytoplankton blooms and superfluous feeding of zooplankton, for instance.

Fig. 2 is an attempt to give a schematic illustration of the position of organic detritus in the pelagic food web. The ingestion of detritus by filter-feeders is not only the exploitation of an additional food resource for them, but must be regarded as a means towards a more effective utilisation of primary production. This is achieved especially in two ways, firstly by the reutilisation of faecal material (see PAFFENHÖFER a. STRICKLAND 1970) and secondly of dissolved organic matter mainly via bacterial growth. Thus it seems possible that this recycling of organic matter, lost at first for herbivores and regained through a repeated ingestion of detritus, makes the energy transfer from primary to secondary producers more effective than usually thought.

To illustrate this idea, food pyramids have been constructed for some stations (fig. 3). The herbivores here include the following size groups: 25 % of the heterotrophs (1 - 150 µ) (comp. p. 4), the size fractions 150 - 300 µ and 300 - 600 µ consisting mainly of copepods and finally the large copepods >600 µ. The other organisms belonging to this size group are presumed to be carnivores. Larger carnivores such as jelly-fish, fish larvae and plankton-feeding fishes are not included here at all. The most striking feature of the diagram is the relatively low standing stock of phytoplankton in comparison to heterotrophic microplankton and organic detritus.

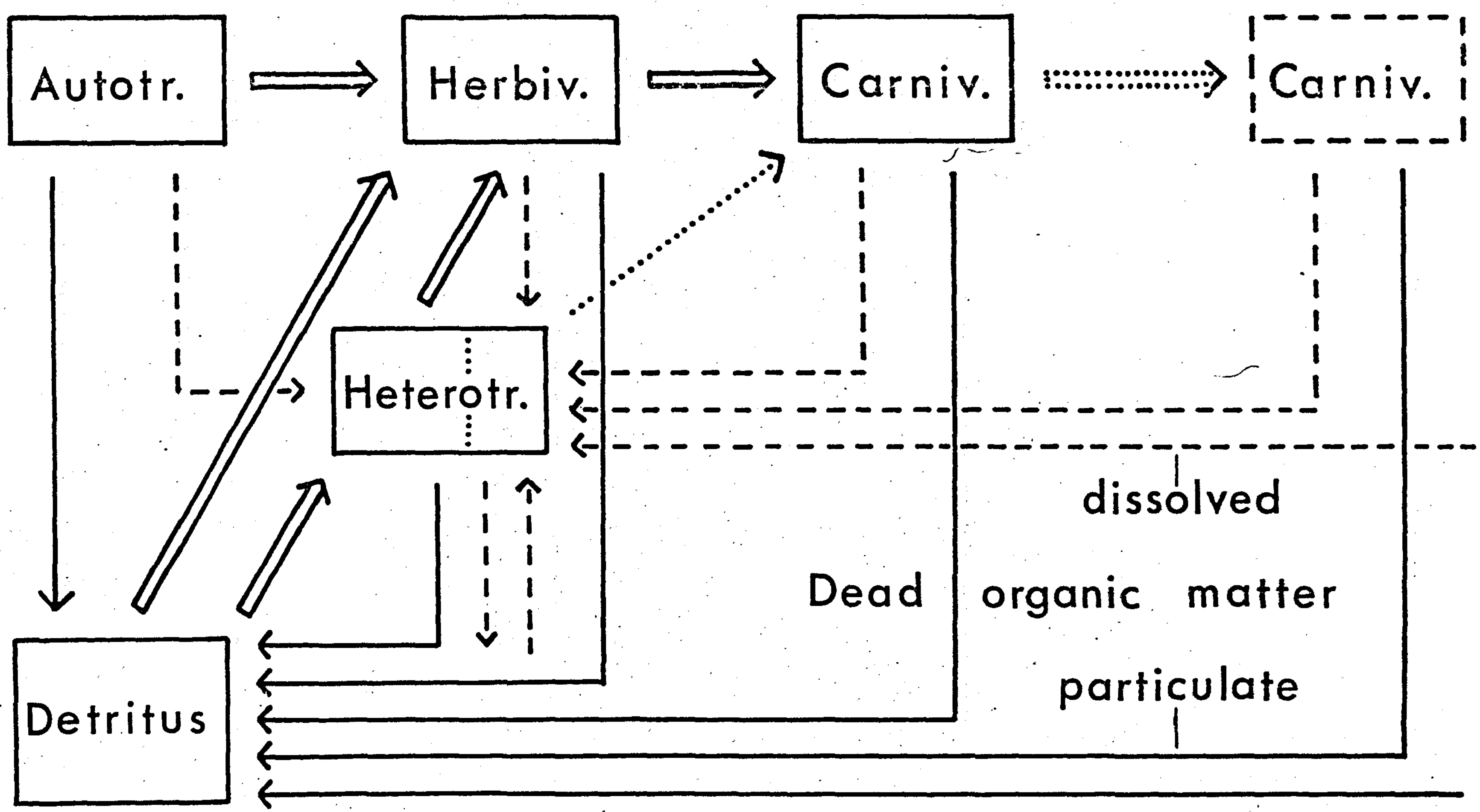

Fig. 2 Schematic presentation showing the cycle of organic matter in the pelagic ecosystem. A third of the heterotrophic microplankton (Heterotr.) is considered "inactive" with regard to food consumption (eggs, cysts etc.). Double and dotted arrows indicate production processes, plain and dashed arrows stand for decomposition processes.

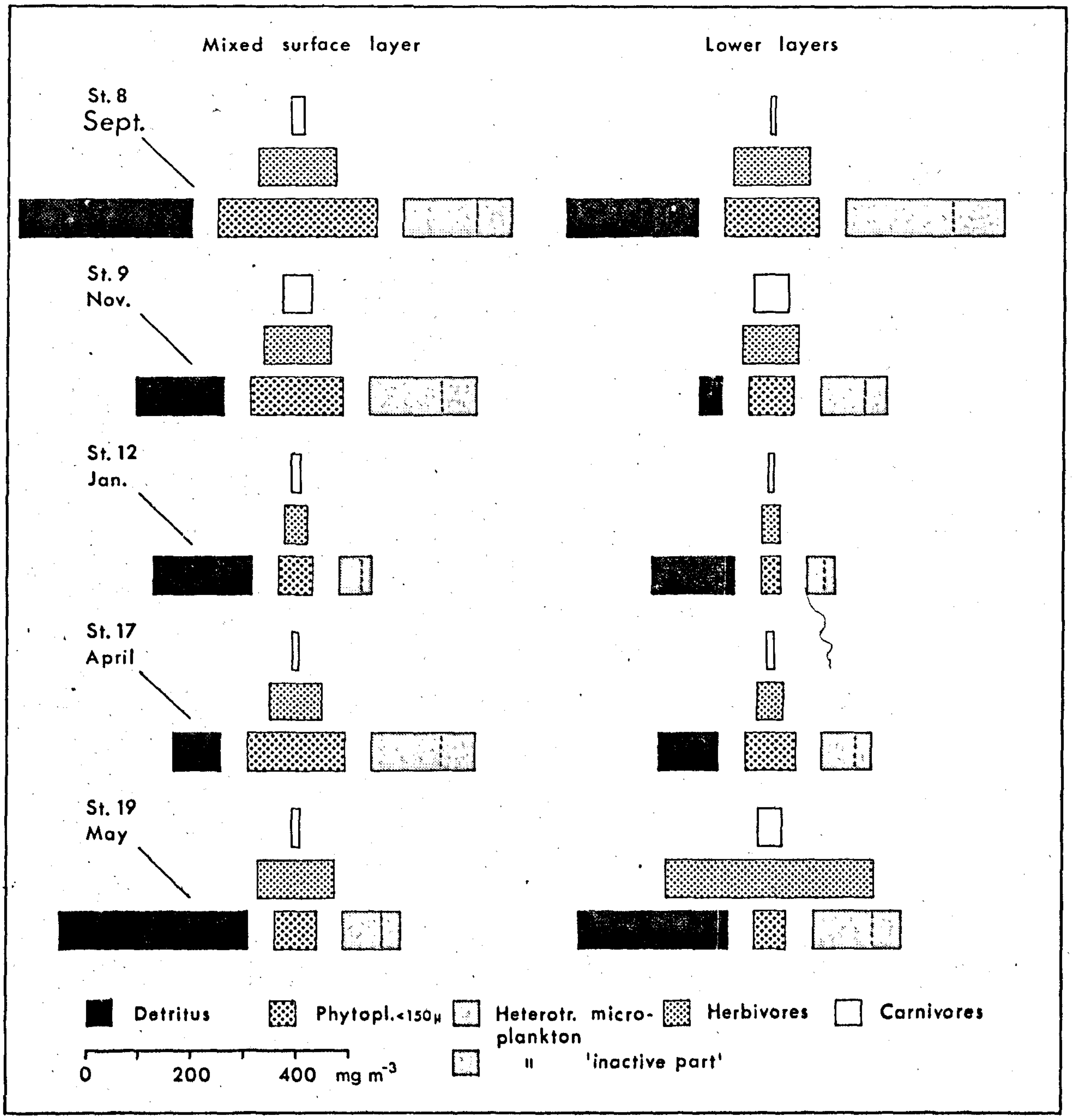

Fig. 3 "Food pyramids" (dry weight of organic matter) constructed for both layers of some stations to illustrate seasonal variation

This observation would appear to endorse the view that in a coastal area like the Western Baltic, herbivores are not forced to rely on phytoplankton alone during most of the year but are able to fulfil their food requirements by the simultaneous consumption of the two other components of organic matter. Pre-supposing this as true, we must also assume that the turnover rates of the latter, especially that of organic detritus, are of the same order as those of phytoplankton. However, this remains to be verified by further research.

S u m m a r y

Particulate organic detritus in the size fraction 1 - 150 μ was measured in 114 water samples taken from different depths in the western Kiel Bight over a one-year period in 1970/71. Grouped into a mixed surface layer and a lower layer according to the main hydrographic features of this area, the results show an annual variation between approx. 100 and 600 mg m^{-3} expressed as dry weight of organic matter. Organic detritus comprises about one to two thirds of the total organic matter in the size class investigated.

Proceeding from the assumption that detritus is indiscriminately filtered by herbivores, it must be accorded an important role in the pelagic food web as an additional food resource. Moreover, feeding on detritus appears to be an effective means of re-utilizing particulate and dissolved organic matter in the upper layers of the sea. This process is thought to heighten the effectivity of the energy transfer from primary to secondary producers.

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