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Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web

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Abstract

The paper examines the conventional notion of the food chain of the oceans in the light of field studies of microheterotrophic processes. In common with the earlier observations of POMEROY (1974), the conclusion is that the classical paradigm is not compatible with contemporary observations and appears to need extending in order to take them into account. The evidence would seem to point towards at least half of primary production passing through the planktonic microheterotrophs before it is mineralized. The possible routes of flow of organic material from the classical food chain (phytoplankton excretion, losses during grazing and zooplankton excretion) were examined in some detail. The conclusions were that the cumulative production of dissolved organic material from the above sources, estimated to amount to about 60 % of primary production, are sufficient to sustain the anticipated rates of microheterotrophic activity. These considerations, by themelves, give no reason to seriously doubt the accuracy of contemporary measurements of primary production. It was calculated, given the present day estimates of microbial growth yields, that secondary production at the microbial level may be comparable to or greater than that of herbivorous zooplankton. When considering the sources of supply of organic material for the microheterotrophs, the events occurring prior to herbivore ingestion were found to be more important than those subsequent to ingestion. As a consequence, the overall accuracy of the estimates of the supply of organic material to the microheterotrophs was very much dependent upon the assessment of total phytoplankton exudation of organic material, i.e. the measured excretion plus that taken up by heterotrophic micro-organisms during the measurement period. The review also highlighted the need for a better understanding of the fate(s) of microbial production: to what extent it is utilized directly by metazoan hervibores as opposed to passing through a protozoan food chain.

Introduction

The present paper will consider the food chain in the planktonic part of the marine environment, and will pose the question: how well do the established notions and conceptual models of the marine food chains of the oceans conform with present day field observations? A reductionist approach will be adopted, whilst at the same time the complexity of the system is recognised. This stance has been adopted because at times in the past plankton research appears to have become lost in the complexity, details and beauty of certain parts of the system and has, as a consequence, overlooked areas of equal or greater importance. At the same time it is recognised that the present approach can be just a distractive.

How do we view the marine food chain? The most lucid and clear account is probably given by STEELE (1974) in his book ''The Structure of Marine Ecosystems''. In this, he provides a brief statement, which perhaps best summarizes the views of many influential thinkers in biological oceanography.

> ''The phytoplankton of the open sea is eaten nearly as fast as it is produced, so that effectively all plant production goes through the herbivores. The animals living on the sea bottom depend on herbivore feces, rather than on a direct fallout of plants, for their food supply. One of the main technical problems in plankton studies has been to demonstrate experimentally that the herbivorous zooplankton can get enough to eat from the densities of phytoplankton found normally in the sea. All indications suggest that herbivores in the sea are resource-limited. On the other hand, there is evidence that these herbivores are highly efficient at transferring energy through the food chain from plants to primary carnivores.''

This quotation indicates the essential points to be considered in the present account. An illustration of the above paradigm is given in Fig. 1. The notion that the main fate of planktonic algae is to be eaten seems to have originated from HARVEY (1945) who provided us with the generalization but, however, gave us little supporting evidence. In this account I will argue that the above generalizations at times seem to be inadequate and at other times wrong.

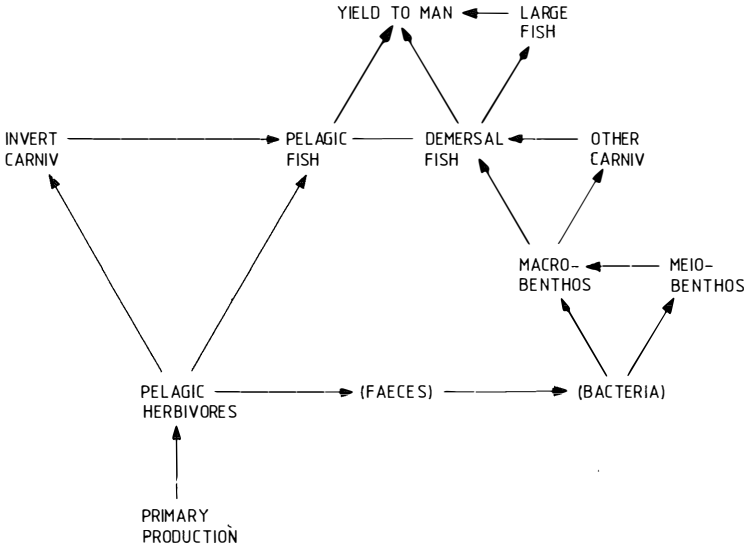

Figure 1
A North Sea food web (redrawn from STEELE 1974)

Identification of a problem

It was Harvey, ironically, who in his work provided us with the clue to the counter-view (ARMSTRONG and HARVEY 1950): that the zooplankton contribution to plankton

metabolism is only part of, sometimes a small part of, overall metabolism. This is implied from the results of a study he made of the mass balance of phosphorus at Station E_1 in the English Channel. The findings are shown in Fig. 2 and they illustrate quite clearly that the major part of organic phosphorus fixed by planktonic algae is lost into the external environment as dissolved organic phoshorus. This was admittedly early work with uncertain methodologies; none the less subsequent studies by STRICKLAND and AUSTIN (1960), DUURSMA (1961), BANOUB and WILLIAMS (1973) and BUTLER et al. (1979) substantially confirmed his original observations. BANOUB and WILLIAMS (1973) illustrated that the effect could be seen in organic nitrogen and carbon as well as organic phosphorus and argued that the studies demonstrated quite clearly that the major fate of phytoplankton production is into the pool of dissolved organic material, only a small proportion being retained by the zooplankton. The implication of these findings is that the organisms which remove the dissolved organic material will play a very major role in the plankton cycle in the ocean.

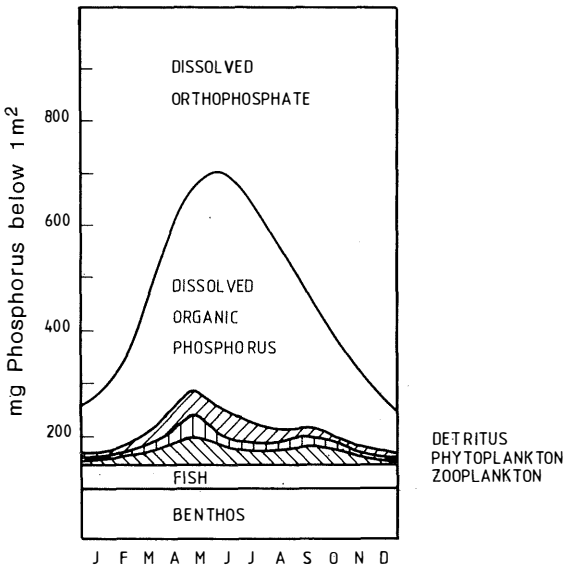

Figure 2
Seasonal phosphorus budget for Station E_1 in the English Channel (redrawn from HARVEY 1965)

There is a second area where problems are encountered by adopting a simple grazing chain model efficiently transferring the products of primary production through the metazoan food web; this is in accounting for the regeneration of inorganic nitrogen in the water column. Table 1 shows data abstracted from a variety of studies. With the exception of the early work of HARRIS (1959), the zooplankton seemed to account for half or less of overall nitrogen regeneration. In coastal water, the usual explanation would be that the material is lost to the sediments and remineralized there. This is implied in the model for the food web of the North Sea produced by STEELE (1974)

Table 1

Calculated zooplankton contribution to phytoplankton photosynthetic ammonia demand

area	NH_3 supplied by zooplankton	source
Long Island Sound	100 %	HARRIS (1959)
Sargasso Sea	10 %	DUGDALE and GOERING (1967)
N.W. Africa upwelling	44 %	SMITH and WHITLEDGE (1977)
N.W. Africa upwelling	55 %	PACKARD (1979)
CEPEX	c. 40 %	HARRISON and DAVIES (1977) & HOLLIBAUGH, et al. (1981).

(Fig. 1). However, the obvious question arises – what happens in the deep sea where the sediments are remote (i.e. over 3 km) from the surface of the oceans? Extensive remineralization is believed to occur in the surface parts of the ocean: for example EPPLEY and PETERSON (1979) have argued that recycled nitrogen accounts for 80 % of the nitrogen used by oceanic phytoplankton. This is consistent with the present estimates of losses from the euphotic zone determined by sediment traps, which suggest (HONJO, 1978; BISHOP et al. 1980) that between 1–10 % of primary production is lost from the euphotic zone, the remainder must be mineralized at the surface parts of the ocean. The conventional explanation is that the 50 % or so of the recycled nitrogen not produced by zooplankton excretions, is mineralized by planktonic bacteria. Although this is a commonly accepted notion its implications do not seem to have been fully recognised. Bacteria, it would appear, grow with an efficiency greater than most other organisms in the food chain. Table 2 contains data illustrating the high apparent growth yield obtained with natural populations of marine heterotrophs; data for zooplankton are included for comparative purposes. Fig. 3 (re-drawn from DEWEY 1976) illustrates the increase in growth yield with decreasing size and complexity. This

Table 2

Estimated growth efficiencies for bacteria

	apparent growth yield	source
Bacteria		
glucose	67 ± 9 %	WILLIAMS (1970)
amino acids	78 ± 8 %	WILLIAMS (1970)
amino acids	50 – 80 %	CRAWFORD, et al. (1974)
amino acids	60 – 95 %	WILLIAMS, et al. (1976)
Zooplankton		
range	3.7 – 50 %	CORNER and DAVIES (1971)
median value	20 %	estimated

could possibly be anticipated on thermodynamic grounds; the greater the level of cellular, bodily and metabolic organisation the less the entropy of the system and accordingly the greater is the amount of energy that has to be spent on building the organisation and thus less available for the organism itself. Thus one would argue that, if we can presume that the present data on the growth efficiency of marine microheterotrophs is reliable and representative, then they will be very inefficient mineralizers. This observation is not new: it was demonstrated experimentally by JOHANNES (1965) that bacteria by themselves effected very little mineralization, this only occurred when protozoa (i.e. a second trophic level) were present. The data in Table 2 taken literally would imply that zooplankton crustacea are more effective mineralizers than bacteria.

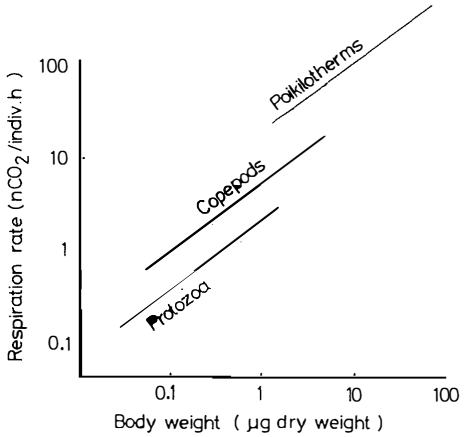

Figure 3

Relationship between respiration rate and body size, for groups of organisms of varying degrees of compexity (redrawn from DEWEY 1976)

The growth yield argument is probably misleading when comparing zooplankton with bacteria because the former, in contrast with bacteria, obviously lose a substantial part of their diet as faecal material, thus net mineralization is not simply the reciprocal of the growth yield, as it is with bacteria. Work with zooplankton suggests that as far as nitrogen is concerned, about 30 % of the diet is mineralized by these organisms. The implications of the above are demonstrated in Fig. 4 with a simple calculation. Assuming, for the sake of illustration, that bacteria and zooplankton mineralize equal amounts of inorganic nitrogen (cf. Table 1) then the organic material consumed by the bacteria would be somewhat greater than that of the zooplankton; however, more importantly, the production of cellular material in the case of bacteria would be somewhat over twice that produced by the zooplankton. Although the calculation is only an exercise, it does none the less illustrate the need to move away from the simple notion of the closed grazing chain comprising algae, herbivores and carnivores, towards a more comprehensive system. This is elegantly summarized (see Fig. 5) by a diagram taken from POMEROY (1974): the part inside the circle is the conventional food chain which has attracted most research activity and interest; the part outside, the rather ill-defined complex of faeces, bacteria, protozoa and the extra-cellular organic pool, is a much neglected part of the food chain.

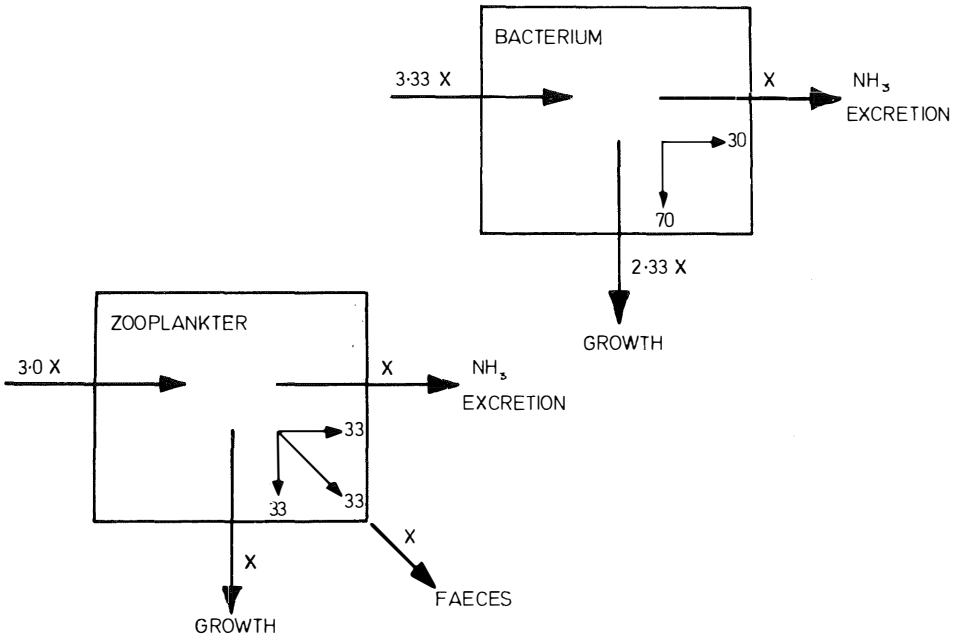

Figure 4

Calculated flow of nitrogenous material through single stage zooplankton and bacterial populations. Bacterial growth efficiency taken to be 70 %. The fate of ingested nitrogen by the zooplankter; one-third to growth, one-third to faeces and one-third to inorganic nitrogen excretion products

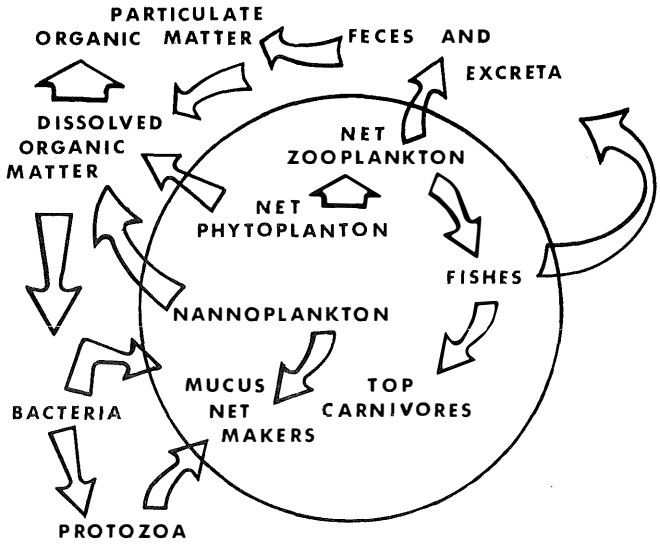

Figure 5

Alternative paradigms of the planktonic food web. The classical view is given in a simplified form within the circle, on the outside it is extended to include the microheterotrophic processes (redrawn from POMEROY 1974)

Evidence for the scale of microbial processes

So far the arguments for the scale of microbial processes have been indirect. What evidence exists? Early studies (e.g. ANDREWS and WILLIAMS 1971), which suggested that perhaps 50 % of primary production was passing through the micro-organisms, were crude in their approach and generally not accepted. SIEBURTH (1977) in summarizing part of the Proceedings of the 1976 Helgoland International Symposium on Ecosystem Research noted a profound difference of opinion between biological oceanographers over the scale of microbial heterotrophic processes; he further commented on the reluctance amongst many biologists to accept the high reported microbial acitivities and biomass.

Through the latter half of the 1970's the evidence for the magnitude of microbial processes and microbial biomass has grown. The patterns in the data are becoming clearer and largely support the earlier pronouncements of marine microbiologists. Table 3 collects together some of the existing data on bacterial biomass and Table 4 is an attempt to derive some indication of the ranges obtained from measurement of the various aspects of the rate of microbial activity in the surface part of the ocean.

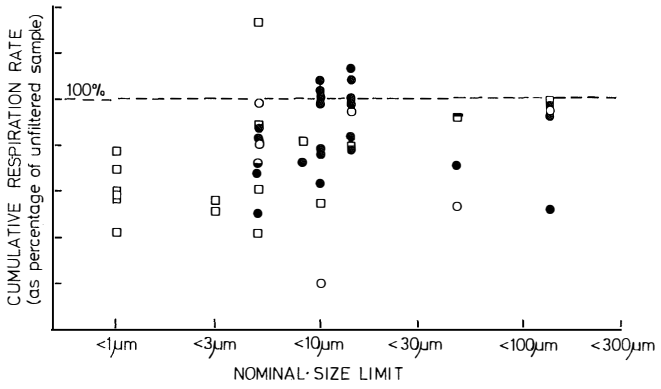

Figure 6

Observed size distribution of plankton respiratory acticity. □ CEPEX, samples from bag; ○ Loch Ewe, samples from bag; ● samples from outside bag. Data are expressed as cumulative respiration up to various size limits, normalized against the rate in the unfiltered sample (details given in WILLIAMS, 1981b)

Table 3

Bacterial numbers in surface ocean water

location	average cell number L^{-1}	
Coastal N. Atlantic	6.6×10^8	FERGUSON and RUBLEE (1976)
Sargasso Sea	2.2×10^8	JOHNSON and SIEBURTH (1979)
Antarctic Ocean	5.4×10^8	FUHRMAN and AZAM (1980)
Californian Bight	4.8×10^8	FUHRMAN, AMMERMAN and AZAM (1980)
mean number	4.8×10^8	
biomass @ 10 fgC per cell	4.8 μg C · L^{-1}	

Table 4
Measurement/estimation of overall growth or metabolism of marine bacteria

growth/biomass increase	median observed rate (μgC l^{-1} day^{-1})	
increase of bacterial numbers in 3 μm filtrates	20	FUHRMAN and AZAM (1980)
growth in dialysis cultures	10 & 250	SIEBURTH, et al. (1977)
frequency of dividing bacteria	10	HAGSTROM, et al. (1979)
ATP increase	10 & 250	SIEBURTH, et al. (1977); SHELDON and SUTCLIFFE (1978)
formation of genetic material		
^{3}H thymidine into DNA	10	FUHRMAN and AZAM (1980)
^{3}H adenine into RNA	30	KARL (1979)
overall metabolism		
oxygen consumption and size fractionation	50	POMEROY and JOHANNES (1966, 1968); WILLIAMS (1981b)
ETS assay	50	PACKARD (1979)
changes in DOC	100 – 250	SIEBURTH, et al. (1977)

Table 5

Calculated distribution of biomass and surface area in CEPEX experimental enclosure CEE-2. Details of the organisms present given in WILLIAMS (1981a). Surface area calculations were made assuming spherical geometry.

organism group	biomass μg dry weight L^{-1}; (% total)	surface area cm^2 L^{-1}; (% total)
bacteria	26 (4.6)	24.6 (69)
protozoa	9.2 (1.7)	0.27 (0.7)
algae	310 (56)	10.7 (30)
copepods: nauplii	2.4 (0.4)	0.03 (0.08)
copepodites	20 (3.6)	0.09 (0.25)
adults	21 (3.8)	0.06 (0.15)
larvaceans	1.2 (0.2)	0.01 (0.03)
gastropod veligers	161 (29)	0.13 (0.36)
zooplankton total	206 (37)	0.32 (0.9)
total	551	35.9

Data obtained at the NSF-IDOE CEPEX research facility and the DAFS Loch Ewe research site illustrate the comparative importance of small organisms (i.e. those less than say 10μm) in overall plankton metabolism. Figure 6 shows the size distribution of respiration within plankton. Although there is inevitably a great deal of scatter, the size distribution clearly does not conform with the established food chain models. The CEPEX data set enabled the distribution of biomass to be calculated and this is given in Table 5 which illustrates that the microbial biomass is comparable to that of the

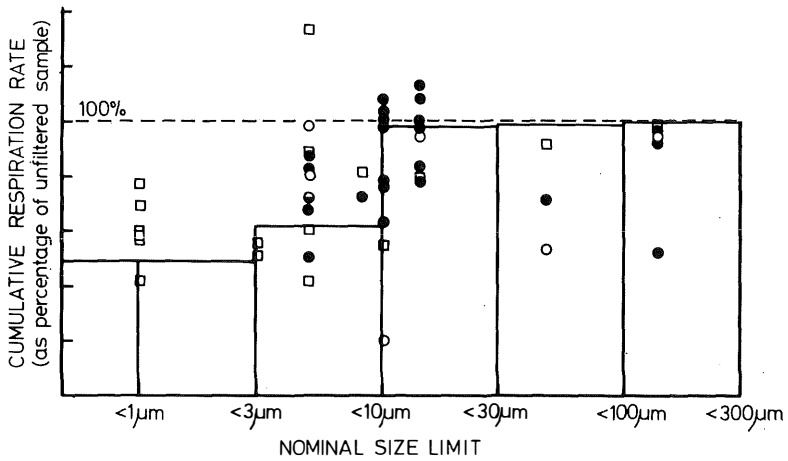

Figure 7

Distribution of plankton respiratory activity with size, calculated from CEPEX plankton abundance records (details given in WILLIAMS 1981a)

herbivorous crustacea in these environments. From the biomass data, using size-dependent equations for metabolic rate, it is possible to calculate the anticipated respiratory rate of the organisms for which data exists and to generate a size distribution of respiration (details of these calculations are given in WILLIAMS 1981 a). The results, an example is given in Fig. 7, illustrate the general agreement between observations and predictions. AZAM (personal communication) has argued that when considering data on the abundance of organisms, the reactive surface areas may be more informative than either biomass (which underestimates the role of the small organisms) or numbers (which clearly overestimates the role of small organisms). Table 5 shows the results of calculation of surface area from the CEPEX data set. The present calculation is recognised to be simplistic: the surface area of the zooplankton is calculated assuming them to be spherical, even so the result of the calculation is sufficiently striking to illustrate the relatively large available bacterial surface area. It would be interesting to make a more thorough calculation, allowing for the exchangeable surfaces of the zooplankton.

Possible solutions to the mass balance problem

Having identified the problem, at least in my own mind, I wish to address the following question. Is it possible to accommodate these observed rates of microbial activity into some conceptual model of material flow through the marine food chain without any radical changes to the existing models? At first sight the problem would seem to have a simple solution: add on the microbial component. Indeed this was in fact considered by STEELE (1974) when he tried to reconcile the high rates of heterotrophic activity, reported by ANDREWS and WILLIAMS (1971), into his food chain model. The difficulty usually encountered with this solution is that the calculated phytoplankton production is scarcely sufficient to satisfy the needs of the herbivores without the added encumbrance of the microheterotrophs (see extract from STEELE 1974). Essentially it appears to be a mass balance problem: insufficient supply or over demand.

Three solutions to the problem may be offered:

1. The presently measured rates of phytoplankton primary production are too low,
2. We can satisfy the apparent needs of both the zooplankton and the microheterotrophs if we look at our existing models more carefully,
3. The present models overestimate the demands of the zooplankton.

I will consider only the first two possibilities here. The first explanation has the advantage of being the simplest. There has been continual criticism of the carbon-14 technique for the measurement of primary production. PETERSON (1980) has recently reviewed the sources of error in ^{14}C technique. It is usual to expect that the errors in the technique will result in an underestimation of phytoplankton production and of course this would allow us to adopt the first of the above explanations. The matter however is more complex than this. First at least one piece of careful work (PETERSON 1978) suggested that the ^{14}C method may *over*-estimate rather than *under*-estimate the rates of phytoplankton production. Secondly, WILLIAMS et al. (1979) when they compared the ^{14}C and the oxygen technique, found a close correlation between the results of the two methods (see Fig. 8). They argued that some of the earlier reported discrepancies between the two techniques, which were originally interpreted as indicating errors in the ^{14}C method, may in fact have stemmed from selection of an inappropriate photosynthetic quotient (P.Q.) by not taking into full account the effect that the nitrogen source has upon the P.Q.

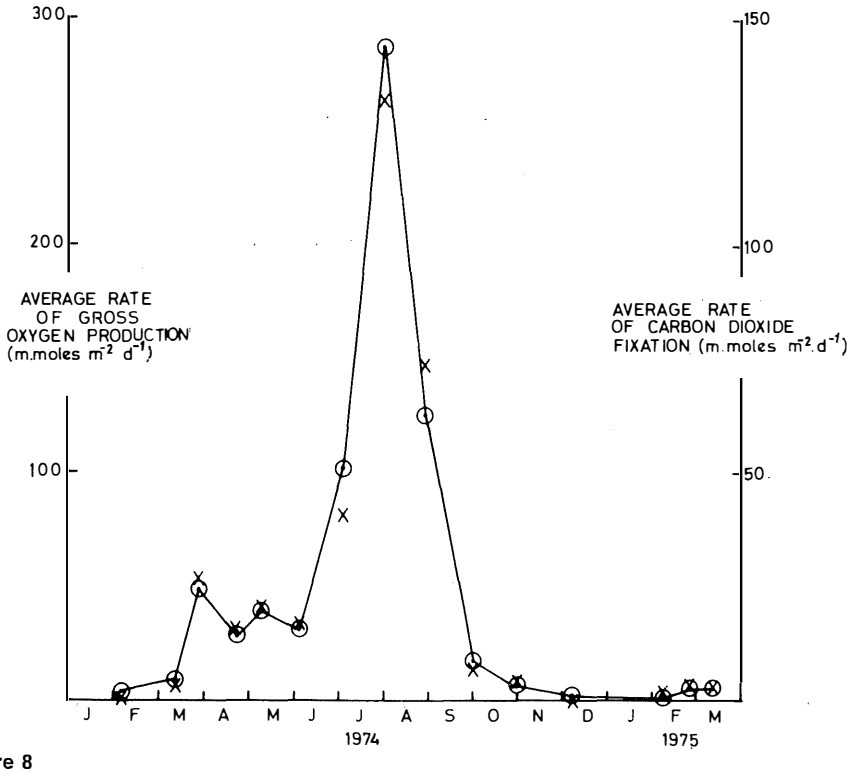

Figure 8

Measured rates of photosynthesis by the oxygen and ^{14}C-techniques. Each data point represents the mean of 18 samples, taken from 3 depths at 6 locations on a transect along the length of Southampton Water. ○: oxygen data, X: ^{14}C data. For clarity only the oxygen data points have been joined up (from WILLIAMS, et al. 1979)

None the less, as Williams et al. (1979) pointed out, this did not constitute proof that the methods were in fact giving the correct answers: for the data in both cases had come from samples incubated in bottles and there have always been suggestions that this could introduce serious errors. GIESKES et al. (1979) for example have demonstrated profound (i.e. tenfold) effects of bottle size on the observed rates of primary production in samples taken from the Tropical N. Atlantic and have argued that their results imply that the present day measurements of the rate of phytoplankton production in ocean water may be severe under-estimates. SIEBURTH (1977) has maintained the same. WILLIAMS et al. (1979) argued that this problem cannot at present be resolved by the ^{14}C-technique, but is open to examination using oxygen as a metabolic parameter. In some exploratory studies, we have attempted to follow diurnal and longer term changes in oxygen production and consumption and to relate them to measured rates of oxygen change in small samples. In a respiration-dominated ecosystem (Fig. 9) a very good agreement between the observed and the calculated rates of oxygen change was obtained. In another system (Fig. 10), where there was a measurable diurnal change, differences were found between the observed and the measured rates but they were nowhere near the scale of effect noted by GIESKES et al. (1979) and could be accounted for as differences arising from experimental error and the lack of correction for advective processes. Thus it would appear, at this stage, that we cannot

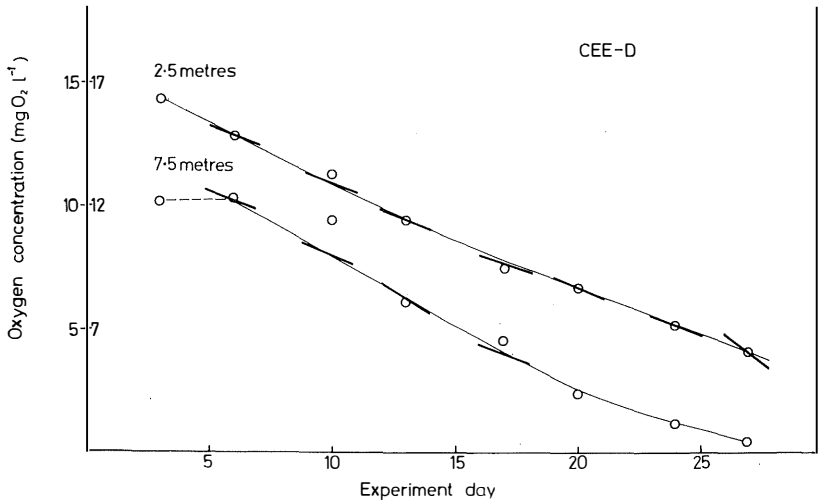

Figure 9

Comparison of measured and observed rates of oxygen consumption in a plankton enclosure at Patricia Bay, Vancouver Island. The thick lines represent rates determined from 18 hour incubations of 125 cc water samples. The continuous line joins up the observed oxygen concentration details given in PARSONS et al. (1981).

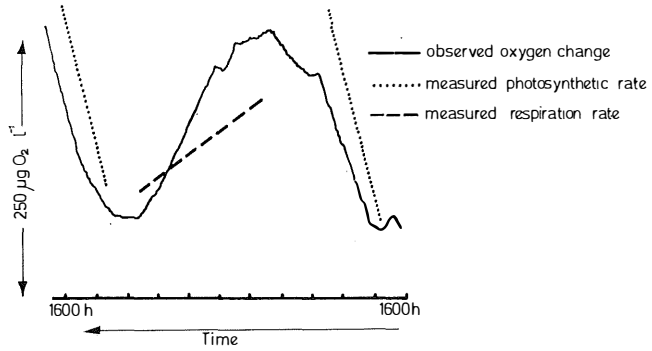

Figure 10

Diurnal profile of oxygen measured in a plankton enclosure at Loch Ewe. The continuous line is an output of an Orbitsphere oxygen electrode, corrected for drift by periodic determination of *in situ* oxygen concentration by Winkler titration

automatically assume that the phytoplankton production rates are wrong and use this as an explanatation to the apparent mass balance problem.

Thus, one turns to the second solution: that the system can supply its needs as it stands if one looks carefully at the routes of transfer of organic material from the grazing chain to the microheterotrophs. First, there is evidence, obtained during the CEPEX experiment, that although we see high rates of microbial activity they, plus the calculated rates of zooplankton activity, can be accounted for within the measured rates of phytoplankton production (Table 6). At least in this one instance, there appears to be no pronounced mass balance problem. This is not an artefact of the CEPEX enclosures, because this situation existed right from the beginning of the experiment.

Table 6

Calculated and observed respiration and photosynthetic rates in the CEPEX experimental enclosure CEE-2. Details of the organisms present and calculations given in WILLIAMS (1981 a)

process and organism group		average rate over upper 10 metres ($mgO_2\ m^{-2}\ day_)$		
			outputs	input
phytoplankton photosynthetic rate (calculated from short term $^{14}CO_2$ incubation)				370
calculated respiration rates				
bacteria			138–276	
protozoa			4.8	
algae			135	
copepods: nauplii	0.9–3.6			
copepodites	3.0–9.5			
adults	1.6–4.9			
sub-total		5.5–18		
larvaceans		0.2–0.8		
gastropod veligers		1.6–5.7		
zooplankton total			7.3–24.4	
total calculated respiration			285–440	
observed total respiration rate			312	
observed microbial (i.e. $<5\mu m$) respiration rate			214	

Organic losses from the grazing chain

Fig. 11 illustrates, in cartoon form, the routes of transfer of organic material from the food chain to the external dissolved organic pool. This pool will be the immediate source of food for the microheterotrophs and will need to sustain their metabolic demands. The aim in the following two sections is to examine the evidence for the scale of the losses from the grazing chain and to see if together they can, in principal, provide sufficient flux of organic material to the external pool to match the observed rates of microbial activity. Loss from the phytoplankton will be considered first.

Exudation of organic material by phytoplankton

Material exuded by the algae during photosynthesis is potentially an important and direct source of organic material for the microheterotrophs and therefore needs careful consideration. There has been extensive work on the study of the exudation of organic material by phytoplankton. Some early studies reported high excretion rates (50–90 %) but as the ^{14}C method of measuring exudation was refined and the sources of error weeded out, lower rates (i.e. 5–20 %) were generally reported (see THOMAS 1971, WILLIAMS and YENTSCH 1976). An extreme stance was adopted by SHARP (1977), who questioned that healthy phytoplankton excreted organic material.

A large proportion of the work on exudation has been, understandably, undertaken with cultures. Some studies, both with cultures (WATT 1966; IGNATIADES and FOGG

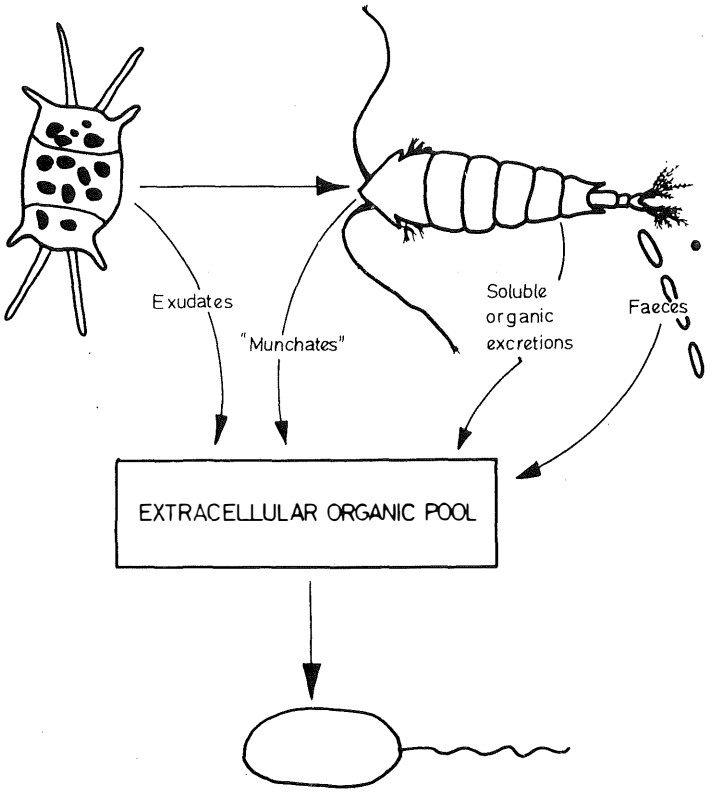

Figure 11

Cartoon of the routes organic flow in the marine plankton from the grazing chain to the microheterotrophs

1973) and with natural populations (ANDERSON and ZEUTSCHEL 1970), have implied an inverse relationship between photosynthetic rate and the percentage exuded. Culture work, which is characteristically undertaken at much higher number densities than exist in natural oceanic populations, could thus give rise to severe underestimates if used for models of natural populations. This fact itself is most likely not important in the present context; however, the mechanism giving rise to the above obversation may be. WILLIAMS and YENTSCH (1976) had noted earlier that ANDERSON and ZEUTSCHEL's data came from samples in which the radioactive counts were very low and that their observation could have resulted from a small systematic error in estimating their control. This criticism does not, however, apply to the culture work. WILLIAMS and YENTSCH (1976) examined the effect in culture, using the same species as IGNATIADES and FOGG (1973) (i.e. *Skeletonema costatum*) and found essentially no changes in the percentage exuded over a range of cell number densities. It was argued by WILLIAMS and YENTSCH (1976) that the discrepancy may have stemmed from a fundamental difference in experimental design. They undertook their work with growing cultures whereas IGNATIADES and FOGG (1973) worked with dilutions of a grown culture. It was suggested that the higher excretions at low cell number densities observed by IGNATIADES and FOGG (1973) may have come from shock occurring during the early stages of adaptation to a fresh medium. This was

confirmed by an experiment undertaken by NAYLOR (1979) who illustrated (see Fig. 12) that in the early stages of growth of a culture in a new medium there was high excretion, the cell number density itself was not the controlling factor. If this initial stress period was allowed to pass, essentially the same percentage excretion rate was obtained through a thousandfold range of population density. The crux of the matter is the type of experimental design which is the most appropriate model for the pelagic system. It may well be that the type of experiment undertaken by IGNATIADES and FOGG (1973) is appropriate to the initial stages of the spring bloom, however once the bloom is underway, the type of experiment undertaken by WILLIAMS and YENTSCH (1976) may be more appropriate. These generalizations can be used to account for the pattern of excretion in the water column reported by such workers as BERMAN and HOLM-HANSEN (1974), who observed high excretion rates at the top and the bottom of the euphotic zone, where one can argue that the population is stressed by high light intensities in one case and low in the other. However, it is arguable if either of these zones are of any great importance in the overall organic economy of the euphotic zone of the sea.

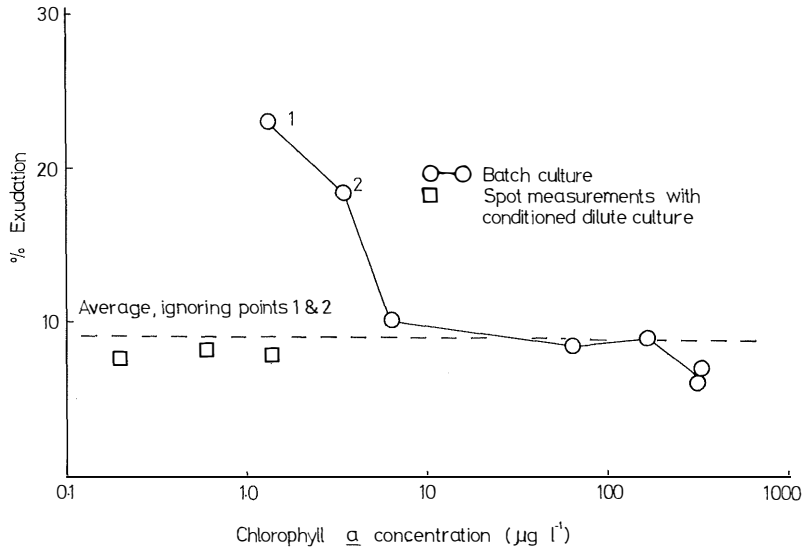

Figure 12

Relationship between the percentage excretion of a culture of *Skeletonema* and culture biomass (as chlorophyll a l^{-1}). Where indicated the cultures were allowed to condition to the new medium for 24 hours before a measurement was made (from NAYLOR 1979)

Characteristically, low to moderate (5–20 %) exudation is reported for the bulk of the water column. However, this is not the end of the problem. It was argued by FOGG (1966) that, in a mixed population of photosynthetic and heterotrophic organisms, one can envisage a mechanism whereby the removal of excreted organics by the heterotrophs would stimulate the rate of excretion by the algae. The material remaining in solution at the end of the incubation will only of course represent net excretion (see. Fig. 13). There have been a variety of attempts to resolve this tight interaction and it is evident that the problem is far from solved. At least four groups of workers have endeavoured to determine the cycling time of the excreted organic

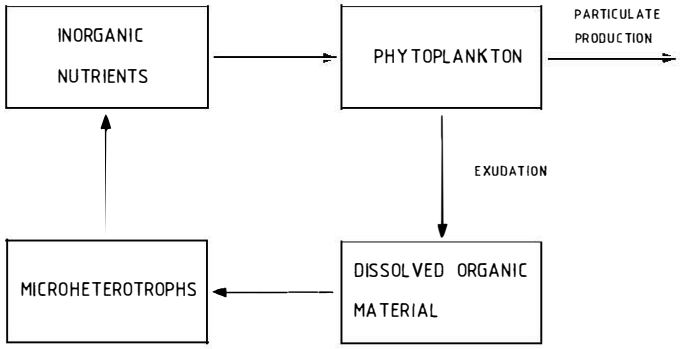

Figure 13
Diagram of the organic cycle involving algae and microheterotrophs

material (WIEBE and SMITH 1977; ITURRIAGA and HOPPE 1977; SMITH et al. 1977; LANCELOT 1979) and their data is summarized in Table 7. DERENBACH and WILLIAMS (1974) and LARSSON and HAGSTROM (1979) attempted to calculate the fraction of primary production taken up by microheterotrophs during a 4–6 hour incubation period, both of these groups used differential filtration as a means of determining the proportion of the photosynthetic products transferred to organisms of bacterial size during the incubation period. The approach is open to criticism (see e.g. BERMAN 1975) on the grounds that the resolution between bacteria and algae by filtration is at best difficult and sometimes impossible, a point noted by DERENBACH and WILLIAMS (1974). None the less, lacking presently other solutions to the problem one has to use the data, whilst at the same time noting the need for caution. The above two groups of workers estimated that during a 4–6 hour incubation period characteristically some 20–30 % of algal primary production was present in organisms of bacterial size. The observed net excretion rates, over such incubation periods, were often only in the region of 10 %. Thus the losses by algae to the dissolved organic pool may well have been in the region of 30–40 % of primary production.

It is perhaps interesting and significant to note in passing, that the estimated turnover times of the excreted fraction (i.e. 10–20 % per hour) seem to be distinctly shorter than those determined by measuring the uptake of ^{14}C-labelled organic substrates. LANCELOT (1979) in his studies, obtained calculated turnover rates of 15 to 39 % per hour; he noted that the rates measured by BILLEN et al. (1980) for a range of organic compounds (aspartate, alanine, lysine, glucose, glycollate, lactate and acetate) were lower by an order of magnitude. If this observation turns out to be correct, then it would imply that either the present radiochemical procedures used to determine the turnover time of organic intermediates are giving incorrect answers or that the wrong compounds are presently being studied. The potential exists, now that sensitive analytical procedures are available, to determine the specific radioactivity of the excretion products and their changes with time, which should provide an alternative way of measuring the turnover time of intermediates in the external cycle of organic material.

There is clearly a call for imaginative work on this difficult problem and a need for new approaches. It will be seen later on that the correct assessment of the fraction of algal photosynthesis ''lost'' to the extracellular pool, is a major factor determining the accuracy of the model of material flow to the microheterotrophs.

Table 7
Estimates of bacterial utilization of photosynthetic products during the incubation period

experimental approach	algal production taken up during incubation	calculated cycling time of exudates h^{-1})	source
differential filtration	1–30 % mainly 15–30 %	—	DERENBACH and WILLIAMS (1974)
differential filtration	27 %	—	LARSSON and HAGSTROM (1979)
analysis of time course experiments	—	0.18	SMITH, et al. (1977)
analysis of time course experiments	—	0.15–0.39	LANCELOT (1979)
analysis of time course experiments	—	0.10–0.12	WIEBE and SMITH (1977)
incubation of labelled excretion products	—	0.08–0.175	ITURRIAGA and HOPPE (1977)

Organic losses by herbivorous zooplankton

The organic events occurring during, and as a consequence of, zooplankton feeding are even more difficult to generalise upon: the nature of the algae food (i.e. flagellates as compared with diatoms) and the feeding mechanism of the organism (i.e. crustaceans as compared with tunicates) will have a profound bearing on the losses from the grazing chain. The balance and emphasis of these various biotypes will vary through the seasonal production cycle. Thus only tentative conclusions can be drawn from the rather sparse experimental work, none the less the exercise seems worthwhile, if only to identify the routes and to emphasise our present areas of ignorance..

Losses of organic material to the external organic pool are known to occur during the feeding due to 'messy eating'. Quantitative data are scarce. LAMPERT (1978) studied the feeding of the fresh water crustacean *Daphnia* and demonstrated that the loss from algal cells swallowed whole was low (about 4 %), whereas losses from large algal cells ranged from 10–17 %. CONOVER (1966) reported that 15 % of the particulate organic carbon removed from suspension by *Calanus hyperboreus* reappeared as dissolved organic material, this was expected to be a consequence of losses from damaged cells and organic excretions by the animal itself. JOHANNES and SATOMI (1967) found that *Palaemonetes pugio* feeding on *Nitzschia* lost about 30 % of the ingested carbon as dissolved organic material.

Similarly, the losses to the dissolved organic carbon pool subsequent to ingestion are poorly characterised: JOHANNES and WEBB (1965) and WEBB and JOHANNES (1967) claimed extensive losses of amino acids from zooplankton; CORNER and NEWELL (1967) and BUTLER et al. (1969) reported that ammonia accounted for about 80 % of the soluble nitrogenous excretion products of *Calanus finmarchicus.* There have been arguments between the two groups of workers over the effect of experimental conditions on the results; CORNER and DAVIES (1971) in a subsequent review suggested that the true figure may lie between the two estimates. We perhaps may thus expect that some 30 % of the excreted nitrogen (i.e. 10 % of the nitrogen in the food intake) will be released as dissolved organic nitrogen.

Finally, there comes the problem of assessing the importance of the faecal material to the planktonic microheterotrophs. This is a complex and, for the enthusiastic scatocologist, a rather fascinating topic. A great deal of attention has been given to the planktonic crustacea, many of which produce pellets surrounded by a pellicle or sheath. The settling rate of these faecal pellets is high: BIENFANG (1980) reported settling velocities in the region of 100 metres per day, with surprisingly little difference between those produced on a predominantly diatom diet as compared with those produced on predominantly flagellate diet. Whether or not faecal material of this type is decomposed sufficiently for it to disintegrate and to retard its descent before passing out of the water column will depend very much on prevailing conditions. This has been discussed by HONJO and ROMAN (1978) who provided the following experimental observations. The surface membrane of faecal pellets from species of zooplankton was found to be degraded within 24 hours at 20–25 °C, at which point the pellet began to disintegrate, whereas at 5 °C the pellets were still intact after 20 days. Thus the temperature and the depth of the upper mixed layer will be critical in determining whether the pellet will lose its pellicle, disintegrate, effectively cease its descent to be decomposed in the upper warm surface water, or whether it will pass through this zone essentially intact. In the latter case it would reach the cold water below the permanent thermocline and only slow decomposition will then occur. As yet our estimates of losses of material in the form of faecal pellets from the euphotic zone are not precise,

numbers in the range of 1–10 % of total production are commonly suggested (HONJO 1978; BISHOP et al. 1980). Such a range would meet with the mass balance requirements for nitrogen in the upper part of the ocean (EPPLEY and PETERSON 1979). In temperate coastal water, little decomposition of copepod faecal pellets would be expected in the water column, for they should reach the sediments within a day of production.

One should not overlook the production of faecal material by the non-crustacean herbivores: tunicates, for example, at times may constitute an important part of the marine plankton. They produce ribbonlike faeces which rapidly become colonised with a rich microflora (POMEROY and DEIBEL 1980). This faecal material makes up an important part of the so-called 'marine snow' and being disperse and possessing a specific gravity close to that of water will tend to remain in the water column and decompose there.

Synthesis

Before attempting to synthesize the above complex of processes, one must recognise that there are probably at least three episodes involving the phytoplankton, zooplankton and microheterotrophs (see Fig. 14).

1. A sudden bloom at a time of low zooplankton numbers. In such situations the bloom is terminated by nutrient exhaustion, rather than grazing. The phytoplankton, once

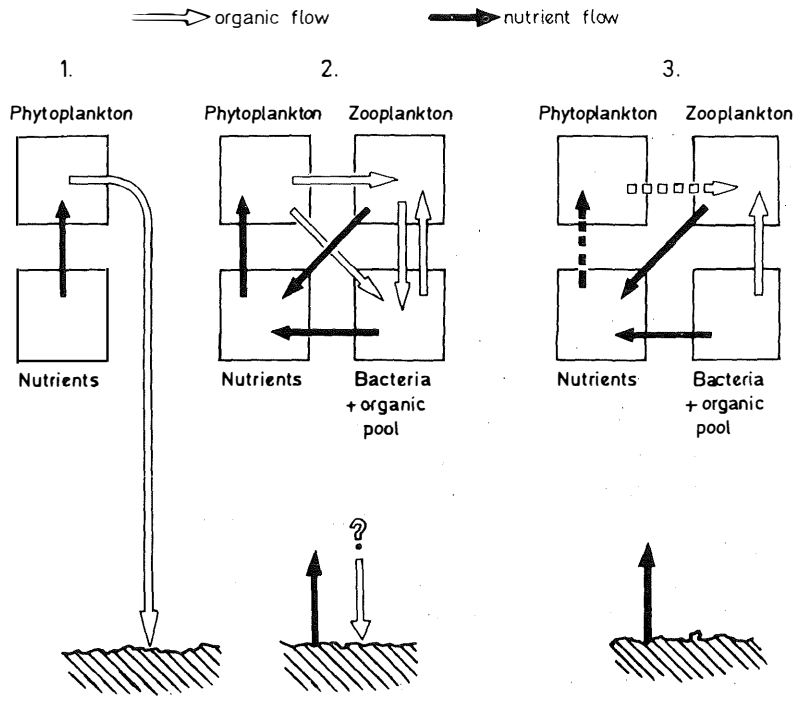

Figure 14

Diagram of three possible episodes involving the phytoplankton, zooplankton, microheterotrophs and the external organic and inorganic pools

nutrient deficient, become negatively buoyant (STEELE and YENTSCH 1960) and sink out of the euphotic zone. This is a very commonly observed phenomenon in enclosed ecosystems. In natural systems it could well be the sequence of events occurring during the spring bloom in temperate regions or in intermittent upwelling regions or in frontal system.

2. A sustained and cropped phytoplankton bloom with active zooplankton and microheterotroph populations recycling nutrients and organic material. This is the situation considered in the present account. The tropical planktonic system and the summer bloom in temperate waters would seem to approximate to this model. The Peru upwelling system would seem to follow a similar pattern (WALSH 1975) except that the zooplankton are replaced by the anchovietta.
3. A period of low phytoplankton numbers and photosynthesis, when the zooplankton energy demands do not seem to be met by the rates of primary production. In such situations the zooplankton may be sustained by the recycling of organic material from the extracellular organic pool by the activities of the microheterotrophs.

I will only consider the second episode. The events described in the first, a bloom and loss of algae to the sediments, appears to be more common than originally anticipated by workers such as Harvey. WALSH (1980) has examined the C/N ratios of sediments from a series of continental shelf habitats around the American continent and concluded that the rapid settling of ungrazed phytoplankton material was a quite widely distributed phenomenon. B. v. BODUNGEN et al. (1980) have studied the phenomenon in a time series in the Bornholm Basin in the Baltic.

To consider the final scene in detail, in my judgement, requires more understanding of the utilization of the organic pool by the heterotrophs and the subsequent fate of these organisms themselves than we presently appear to possess. Thus it will not be considered in the present account, not because it is ecologically unimportant but because of the present lack of information.

The next step is to put together the observations made earlier in this paper, into some tentative model to see if it will supply the estimated needs of the microheterotrophs, i.e. half or more of the products of phytoplankton production. The calculation is illustrated in Fig. 15. The philosophy has been to adopt median values where available and where doubts exist a conservative estimate is taken. One would therefore expect to end up with an under-estimate, rather than an over estimate, of the flow of organic material to the microheterotrophs.

The steps in the calculation are briefly as follows:

1. It will be presumed, following HARVEY (1945) and STEELE (1974), that all phytoplankton cell production is taken by the herbivores.
2. Direct losses by the phytoplankton: a figure of 30 % is adopted for the total loss, this is intended to take into account the rapid utilization of the exudates by the microheterotrophs.
3. Losses during grazing: a figure of 15 % of the plant material taken by the zooplankton is presumed to end up as spoilage in the form of dissolved organic material.
4. Zooplankton feeding efficiency: the apportionment between assimilation, solid excretion products and dissolved excretion products is taken to be equal.
5. Zooplankton-originating dissolved organic excretion products: of the soluble excretion products from the zooplankton, 30 % are assumed to be organic. This is

somewhat greater than the figure estimated by CORNER and NEWELL (1967), but is thought to be in keeping with the suggestion of CORNER and DAVIES (1971).

6. Water column decomposition of faecal material: it will be presumed that 50 % of the faecal material settles out of the water column and the remainder is decomposed in the water column itself. One might expect a greater percentage of crustacean faecal material to settle out, but some consideration has been given to faecal material of non-crustacean origin.
7. Microheterotroph growth efficiency: the heterotrophs are presumed to have a growth efficiency of 70 %.

These calculations (see Fig. 15) imply that perhaps 56 % of primary production may be funnelled to the microheterotrophs if the food chain up to the herbivores is considered. The primary carnivores and the higher trophic levels may provide a further 10 % or so, giving a total figure in the region of 60 % of primary production passing onto the heterotrophs.

Conclusions from the calculations

The conclusions one can draw from the present exercise (and one must stress that it is only an exercise) are as follows:

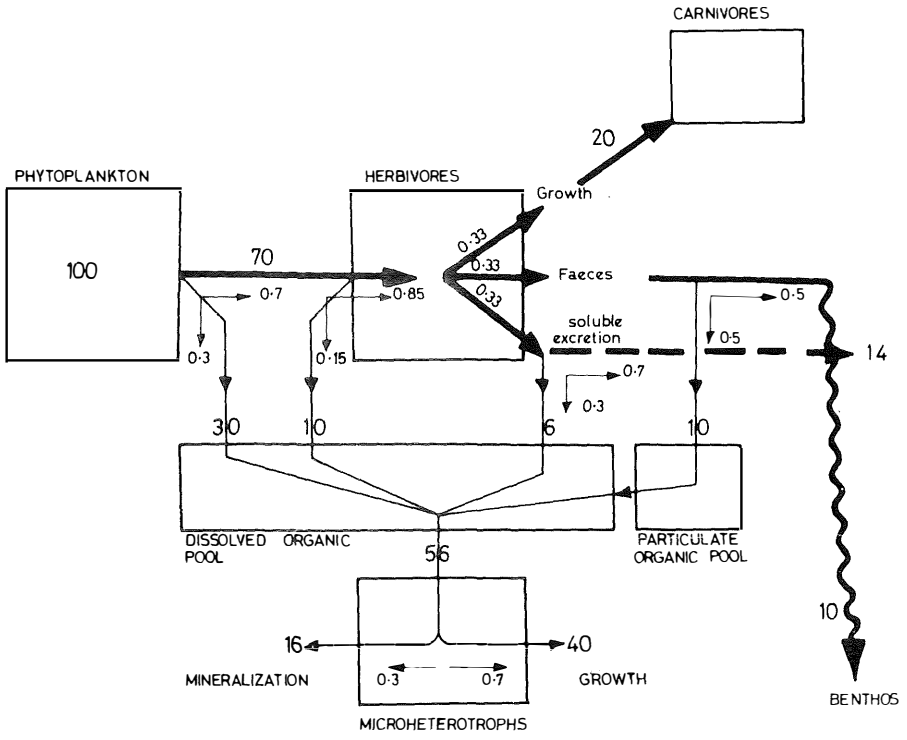

Figure 15

Calculation example of the flow of organic material through the planktonic system. Details are given in text. The large numbers refer to the calculated percentage of phytoplankton production passing along a particular route. The smaller numbers, normally associated with the finest lines, indicate the fractional flow along alternative pathways

1. It is possible to envisage an amount, equivalent to 50–60 % of primary production passing to the microheterotrophs via the extracellular organic pool without any severe meddling with the existing food chain models. The estimate of 50–60 % could be low: for conservative estimates have been used where alternatives existed.
2. Equal amounts of inorganic nitrogen regeneration are attributed to the microheterotrophs and the herbivorous zooplankton. This is in keeping with field data (Table 1). The calculation for the zooplankton is not explicit in Fig. 15, but would be calculated to be equivalent to 14 % of phytoplankton production (i.e. 0.7 x 20 %).
3. Perhaps most interestingly the ''model'' illustrates that the microheterotrophs may pass on twice as much organic material to the next trophic level as the herbivorous zooplankton.
4. The flow to the microheterotrophs is controlled more by events occurring prior to zooplankton food ingestion than after. Thus the accuracy of the present calculation is heavily dependent upon the value used for the extent of exudation of organic material by the phytoplankton.

One should note in passing a somewhat similar model proposed by VINOGRADOV, et al. (1973) for a pelagic tropical ecosystem. They estimated that about 70 % of the energy flow passed through bacteria. Direct comparison of the two ''models'' is not entirely justified because their model, quite correctly, took into account the recycling of material due to secondary production, thus values greater than 100 % can be obtained in their case.

The present exercise points out very clearly that if one wishes to understand the dynamics of the food web, it is necessary to establish the trophic fate of ''microbial production''. The key issue is to determine to what extent the products of microbial production pass through a several step protozoan-type food chain, a consequence of which would be that the microbial production will be largely remineralized before it reaches the herbivore level (but see HEINBOCKEL and BEERS 1979). Alternatively, there is the possibility of direct utilization of bacteria by herbivorous zooplankton: for

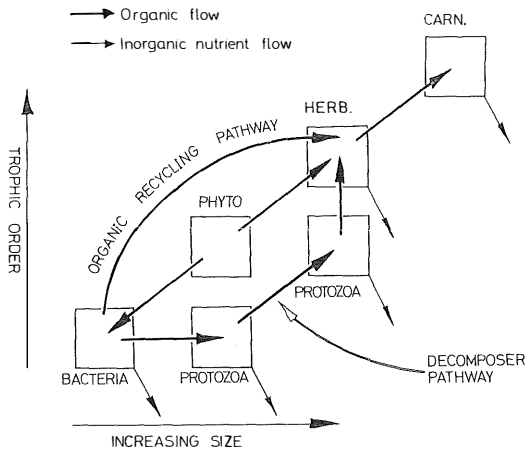

Figure 16

Diagram illustrating the potential trophic differences between the decomposer pathway and the organic recycling pathway in the marine plankton

example, KING et al. (1980) have demonstrated and studied the utilization of natural assemblages of planktonic bacteria by the tunicate *Oikopleura dioica*. PARSONS et al. (1981) found indirect evidence for the transfer of organic material from organisms of bacterial size to herbivore size, without clear sign of passage through organisms of intermediate (i.e. protozoan) size.

The point is made in Fig. 16, that if the fate of microbial production is to the classical decomposer pathway, then it is largely remineralized en route and thus the microbial complex (rather than the bacteria alone, which is the common misconception) acts as remineralizing unit, and the activities of the microflora will have a lesser impact on the trophodynamics of the grazing chain. In such a situation the ''Steele-Harvey'' model would describe the essential aspects of the flow through the food chain even though there was extensive simultaneous microbial organic metabolism. On the other hand, if the ''recycling loop'' predominates then there will be a substantial supplementation of the food chain by the loop and some rethinking of the trophic structure will be necessary. It may point to two niches at the herbivore level: those capable of predating upon the medium to large sized algae and those capable of gathering organisms of bacterial size, or more likely supplementing their diet with these organisms.

Overall conclusions

What general conclusions can be drawn from the present study?

1. Existing field observations make it difficult to accept a tightly closed grazing chain with only a small organic flow to the microheterotrophs.
2. If we accept the present estimates of losses from the grazing chain, it is possible to envisage sufficient flow of organic material to the extra cellular organic pool to sustain the presumed activity of heterotrophic microorganisms in the plankton.
3. The calculated flow of organic material to the microheterotrophs is heavily dependent upon the value used for exudation of organic material by the phytoplankton.
4. The data needed to assemble and examine a model of organic flow to the microheterotrophs comes mainly from studies of coastal ecosystems and it is possible that profoundly different patterns may be observed in other environments, such as upwelling areas or oligotrophic waters.
5. The amount of organic material made available to the next trophic level by planktonic bacteria, could be comparable to or greater than that made available by the herbivores to the primary carnivores.
6. Understanding the trophic fate(s) of heterotrophic microorganisms is the key to determining whether the microbial complex acts as a mineralizing or an organic recycling unit.
7. There is no evidence to presume that, in coastal waters, microbial activity is occurring exclusively in the sediments, the water column appears to play an important role.

In many respects the present paper has reiterated the earlier conclusions of POMEROY (1974) although with the advantage that the data which has accumulated in the interim period has made the argument easier to present.

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