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Report of the workgroup "Organic Matter", 1977-1978

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Introduction

For the last few years, we have attempted to describe and understand the ecometabolism of some biocenoses in the Southern North Sea. In this synecological approach, it was necessary to determine the main characteristics of the carbon and nitrogen cycles: biomasses and concentrations, fluxes and activities. A summary of the results of this team work has been published (Billen et al., 1976) . In this paper, the authors gave a general picture of the ecometabolism of the visited ecosystems, and raised some new problems, mainly concerning the planktonic phase. The group "Organic Matter" took as a goal, in 1977, to try to solve these problems.

0.1.- CONSISTENCY OF THE RESULTS OF PRODUCTION AND CONSUMPTION

The construction of the carbon budget revealed an important contradiction : in the absence of any significant import of exogenous organic matter, the only source of organic carbon consists in primary production. However

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the results obtained in the Sluice-Dock of Ostend showed that the account was unbalanced, and that there was a contradiction between the amount of organic matter formed by gross primary production and the amount used by consumers; consumption was almost twice as high as production. In the Southern Bight of the North Sea, consumption is 10 to 20 times higher than production. This means that either the gross primary production had been underestimated, or the consumption overestimated (see Joiris, 1977 a,b).

In order to solve this contradiction, we had to verify the measurements of high planktonic respirations on the one hand, and gross primary production, on the other hand.

Within the values of respiration, we had to determine whether our supposition, that bacterioplankton indeed plays the main role, was correct. This means that we had to try to determine the real (i.e. *sensu stricto*) heterotrophic activity through the use of other independant methods.

In the case of primary production, two factors could lead to an underestimation: the production of soluble (excreted) organic matter with such a high turnover rate that it could be respired during the incubation, and/or a phytoplanktonic respiration with much higher values than earlier calculated.

0.2.- THE RECYCLING ROLE OF ZOO- AND BACTERIOPLANKTON

Another important remark to be drawn from the same results concerns the relative importance of zooplankton and heterotrophic microorganisms (mainly bacteria) in the utilization of the phytoplanktonic production. In contradiction to the classical scheme of a "complete" food web: producers - - herbivors - carnivors, the study of the coastal biocenoses of the Southern North Sea indicated that the bacterioplankton played a prominant role in the recycling of the produced organic matter. This aspect of the discussion was however obscured by the contradiction between production and consumption figures, and needed to be confirmed by new measurements.

0.3.- COMPARISON OF DIFFERENT BIOCENOSES

The description of ecological structure of the coastal biotopes in the Southern Bight can be completed with some results from other regions in the North Sea. All results can be framed in the following hypothesis: the Atlantic water coming into the North Sea through the region of the Shetlands is characterized by a complete food chain: primary producers - zooplankton - fish - pelagic seabirds; bacteria only in very low amounts. In the central North Sea, on the contrary, one fimds a bacterial by-path to the normal food chain; seabirds are scarce, but bacteria are much more abundant (Joiris, 1978).

A confirmation of the role played by zooplankton in the northern Atlantic water was obtained in the Fladdenground (Flex 70): the variations of the phytoplankton standing-crop could be entirely explained by the measured values of primary production and the measured grazing of zooplankton on living phytoplankton (Daro, 1979).

We considered therefore it would be worthwhile in trying, not only to confirm the importance of bacterial recycling in North Sea waters, but

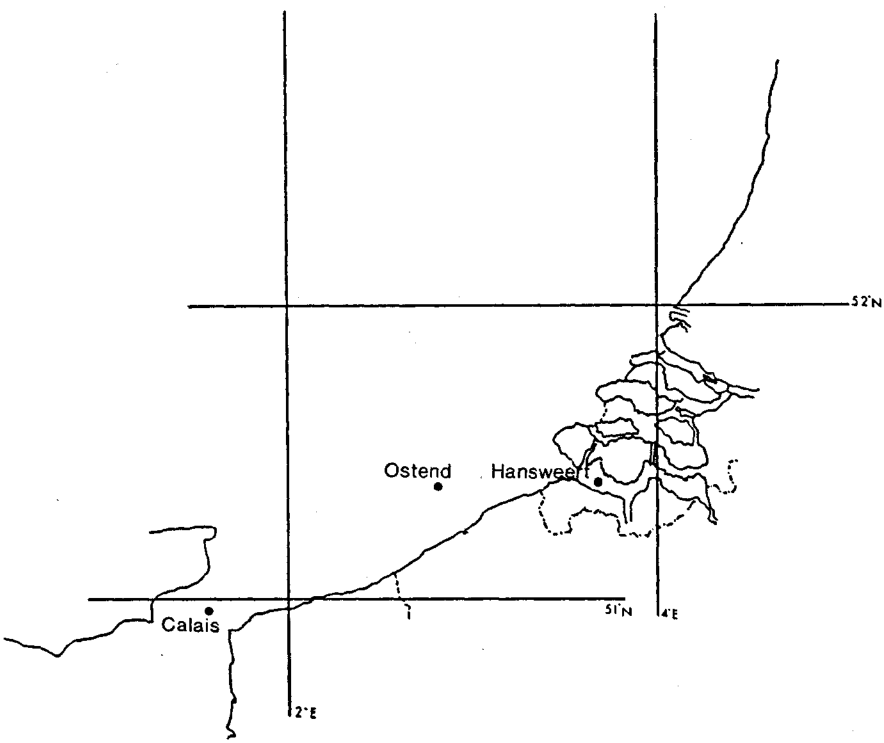

fig. 1.
Position of the sampling stations visited

also to use the same methods for evaluating the stocks and fluxes in Atlantic water. For practical reasons, such as the lack of adequate ship facilities, we were not able to reach the northern Atlantic water. As an alternative solution, we looked for a water mass with "Atlantic" characteristics in the English Channel.

Finally, a third biotope was added in the programm: the Scheldt estuary, since a completely different ecological structure was to be expected there. These three stations are representative of the main types of biocenoses in the North Sea: estuary, coastal sea, open sea.

The position of the three stations is as following (see fig. 1):

1. North Sea water : station "Ostend" 51°24'N, 2°48'E
2. "Atlantic" water: station "Calais" 50°57'30"N, 1°23'30"E
3. Scheldt estuary : station "Hansweert" : 35 km from the open sea.

The experimental work was done on board of the *RV Mechelen* (coordination : H. Picard) and, on two occasions, on board of the *RV Friedrich Heincke* : 7 - 10 October 1977 (coordination : P. Weigel) and 7 - 18 April 1978 (coordination : W. Hickel).

1.- Methodology

In the previous investigations, use was made of rather crude methods for the determination of fluxes, namely :

- measurement of $H^{14}CO_3^-$ incorporation for estimating particulate net primary production with the classical Steeman-Nielsen (1952) method;
- measurement of initial dark oxygen consumption for estimating total planktonic respiration;
- calculation of zooplankton ingestion from the biomass of each zooplankton species and development stage, and their "daily food requirement" compiled from the literature.

The results presented here are based on a refined methodology achieving a more detailed speciation both of the stocks of organic matter and of the fluxes they undergo. This methodology was developed in order to approach more closely the basic nature of the biological processes involved in the relationships:

1. phytoplankton - organic matter - bacteria
2. phytoplankton - zooplankton

1.1.- PHYTOPLANKTON — DISSOLVED ORGANIC MATTER — BACTERIA RELATIONSHIP

Among the huge diversity of organic substances produced by phytoplankton and constituting dissolved and particulate organic matter, only a small part can be directly taken up and used by microorganisms.

Dialysis or ultrafiltration of dissolved organic matter in seawater reveals indeed that it is mostly made of macromolecules with molecular weight higher than 500 (Ogura, 1974). Now, only low molecular weight organic molecules can be directly taken up by bacteria. Therefore, the pool of directly usable organic matter is constituted by the pool of low molecular weight organic molecules, which is alimented either by direct excretion by phytoplankton, or by exoenzymatic hydrolysis of macromolecules or particles.

These considerations have led us to focus the measurements on directly usable organic substrates, their production and consumption rates.

A method was developed for measuring dissolved primary production. It involves the kinetic measurement of labelled dissolved organic matter produced during incubation with $H^{14}CO_3^-$ in the light and simultaneously allows an estimation of the rate of microbiological consumption of the excretion products (Lancelot, submitted). Ultrafiltration of the excreted organic matter also allows a first speciation of the dissolved organic matter produced. The results indicate that about 30 - 50% of the excreted organic matter is made directly usable compounds (MW < 500) (Lancelot, submitted).

Apart from the determination of the overall organic matter concentration (TOC, BOD_5) numerous dissolved - directly usable - organic substrates in seawater were determined: individual free amino-acids, glucose, glycollate, lactate and acetate. From these measurements, a tentative estimation of the total pool of directly usable organic substrates was made (Billen et al., submitted).

The rate of utilization of these substrates was also determined by adding high specific activity ^{14}C labelled molecules and studying their uptake kinetics and their respiration (Billen et al., submitted).

A tentative estimation of *sensu stricto* heterotrophic activity (excluding intracellular phytoplanktonic utilization of their own photosynthetized substrates) was derived from these measurements.

1.2.- PHYTOPLANKTON — ZOOPLANKTON RELATIONSHIP

Zooplankton nutrition can occur either on living phytoplankton, on detritus and bacteria or on accumulated lipid reserves. These three modes of nutrition have of course quite different effects on the dynamics of the system.

Grazing on living phytoplankton was determined by incubating zooplankton with pre-labelled natural phytoplanktonic populations and counting the radioactivity ingested (Daro, 1978).

Speciation of particulate primary production was achieved through biochemical fractionation of the radioactivity incorporated during incubation with $H^{14}CO_3^-$. Comparison of these data with the biochemical composition of living phytoplankton and detritus provides indications on the relative utilization rates of the various particulate biochemical constituents (Lancelot, in prep.).

Biochemical composition of zooplankton was also determined, providing evidence of the constitution of lipidic reserves by these organisms (Hecq, and Gaspar, in prep.).

Zooplankton density was also determined species by species and development stage by development stage. When available analysis of time series of such data allows the determination of the population dynamics parameters of zooplankton (Bossicart and Mommaerts, in prep.).

2.- Results and discussion

A summary of the results to be used in the general discussion is presented in table 1 and in figures 2, 3 and 4. This constitutes the basic information for the discussion of the three problems presented in the introduction:

- coherence of production and consumption measurements
- relative roles of zooplankton and bacterioplankton
- comparison of three different biocenoses.

Table 1

Summary of the results obtained in the Belgian coastal zone (zone 1S) (1973-1975) and at the stations "Ostend", "Calais" and "Hansweert" (1977-1978)

	Method[a]	Units	Belgian coastal zone[b]	Station "Ostend"			
				mean	min	Max	(n)
Phytoplankton biomass	1	mgChl/m^3	7.93	7.35	2.77	21.50	(10)
Primary production							
net particulate	2	mgC/m^{2}day	293	362	251	474	(2)
net dissolved	2	"	(122)	98	30	172	(2)
net total	2	"	(415)	460	281	636	(2)
gross (30% respiration)	0	"	(593)	(658)			
(50% ")	0	"	(830)	(920)			
Zooplankton							
biomass	3	mgC/m^3		7.30	0.29	22	(5)
grazing	0	mgC/m^{3}day	19.4				
	2	%stock/day	–	5			
respiration	4	mMO$_2$/m^{3}h.	0.015	0.015			
Planktonic respiration	4	mMO$_2$/m^{3}h.	5.25	0.67	0.13	1.00	(3)
				3.20[c]			(21)
Heterotrophic activity	5	mgC/m^{3}h.	–	2.50	0.86	17.60	(22)
-respiration (2/3)	5	"	–	1.67			
-assimilation (1/3)	5	"	–	0.83			

	Units	"Calais"				"Hansweert"			
		mean	min	Max	(n)	mean	min	Max	(n)
Phytoplankton biomass	mgChl/m^3	1.02	.34	2.25	(6)	7.38	4.48	18.51	(7)
Primary production									
net particulate	mgC/m^{2}day	163	117	260	(3)	15			(1)
net dissolved	"	49	40	58	(2)	2			(1)
net total	"	212	157	318		17			(1)
gross (30% respir.)	"								
(50% respir.)	"	(424)				(34)			
Zooplankton									
biomass	mgC/m^3	2.50	.17	9.0	(5)	–			
grazing	mgC/m^{3}day	–				–			
	%stock/day	6				–			
respiration	mMO$_2$/m^{3}h.	0.02				–			
Planktonic resp.	mMO$_2$/m^{3}h.	0.37	0	2.55	(13)	1.13	1.10	1.15	(2)
Heterotrophic activity	mgC/m^{3}h.	0.33	0.04	1.88	(20)	8.45	4.28	14.50	(5)
-respiration	"	0.22				5.64			
-assimilation	"	0.11				2.81			

a. Methods : 0 = calculated; 1 = chlorophyll; 2 = ^{14}C-bicarbonate incorporation; 3 = counts; 4 = oxygen consumption rate; 5 = incorporation of labelled substrates.

b. From Billen et al., 1977.

c. Mean value from 21 determinations in the coastal zone (not only Ostend), 1977-1978.

(n) : Number of determinations.

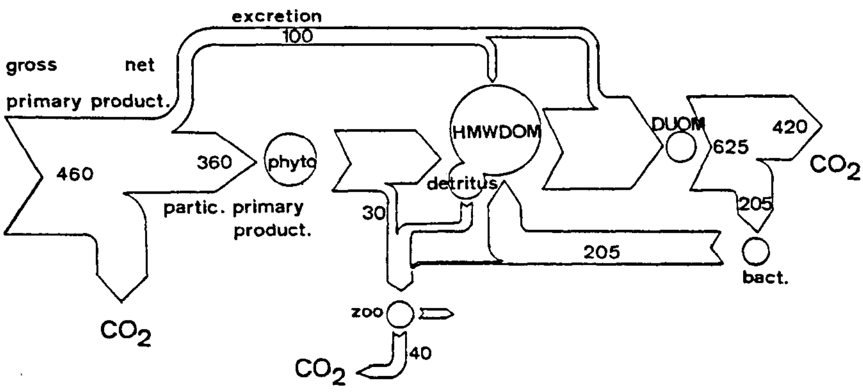

fig. 2.

Circulation of carbon between the first trophic levels at the station "Ostend".
(All fluxes in mg C/m² day.)
Abbreviation : HMWDOM : high molecular weight dissolved organic matter.
DUOM : directly usable organic matter.

2.1.- COHERENCE OF PRODUCTION AND CONSUMPTION MEASUREMENTS

Different approaches can be used, in order to solve the contradiction between the values of gross primary production and total consumption. This discussion concerns first of all the results obtained at the station "Ostend", and the results obtained earlier in the same zone ("zone 1 South") of the southern Bight.

2.1.1.-

A first remark to be made is that, generally speaking, the values obtained in 1977 and 1978 at "Ostend" can very well be integrate into the mean values obtained in the previous years for the zone 1s with much greater sampling. This allows us to consider that the new results are sufficiently representative of the real situation, even though the number of samples is rather low.

2.1.2.-

The estimation of the planktonic heterotrophic activity (*sensu stricto*) obtained by adding up the several specific utilization rates gives, of course, strictly minimal figures, since there is always a possibility that some substrates, which had not been measured, play a significant role.

At the station "Ostend", this flux of heterotrophic activity reaches a value (625 $mgC.m^{-2}day^{-1}$) comparable with the net primary production (460 $mgC.m^{-2}day^{-1}$). The respiratory fraction was measured as 2/3 of the heterotrophic uptake and reaches the same value (420 $mgC.m^{-2}day^{-1}$) as the primary production.

The comparison between heterotrophic activity and dissolved primary production clearly shows that the phytoplanktonic excretion (100 $mg C.m^{-2}.day^{-1}$) cannot be considered as the main source of organic matter for the heterotrophic microorganisms (the bacteria). Therefore, other mechanisms, such as phytoplanktonic mortality, must be considered since all the produced organic matter must be made available for the heterotrophic organisms.

2.1.3.-

In order to explain the contradiction between production and total consumption, the dissolved primary production must be very important and the produced substances had to show a very high turnover rate. The mean value for excretion is not very high, being about 25% of the particulate primary production; the linearity of the kinetics implies that there is not a high turnover rate for the excreted substances. However, it is worth noticing that, in a few cases, turnover rates up to 40% per hour were detected, indicating the possible existence of one or several substrates not yet detected by the methods presently used. If such results are confirmed later, it would be very important to identify and study these substances.

A special discussion must be devoted to glycollate: it is generally considered to be the main excretion product of marine phytoplankton and represent 9 to 38 % of the total excreted amount (Hellebust, 1965). This is confirmed by the fluxes we measured: from the measurements of heterotrophic utilization of glycollate, a flux of 36 $mgC.m^{-2}day^{-1}$ was measured at Ostend (29 at Calais), or 37 % of the dissolved primary production (59 % at Calais).

In terms of turnover rates, however, the utilization by bacteria is rather low: 0.27 % h^{-1} at Ostend, 0.06 % at Calais. Therefore glycollate cannot be the hypothetical excretion product utilized at a very high turnover rate that we are looking for.

2.1.4.-

We still need more measurements to confirm the results before a definitive conclusion can be drawn, but the general impression is that a series of values can be considered as being correct:

- the net particulate and dissolved primary productions,
- the planktonic heterotrophic activity (*sensu stricto*),
- the efficiency of the heterotrophic microorganisms (about 33 %).

It follows that all results, including those that are apparently inconsistent (production versus consumption), together fit well on the condition that the simple hypothesis proves to be correct, i.e. that the respiration of the autotrophic organisms (the phytoplankton) is much higher than estimated in the earlier calculations. Hence the gross primary production would be much higher than estimated earlier, and that the carbon cycle would be equilibrated.

The research program for the next years will give a priority to more direct methods for the assessment of phytoplanktonic respiration.

It must however be born in mind that another possibility cannot yet be totally excluded, even though we consider it highly improbable, i.e. the existence of an organic substance excreted by the primary producers and very rapidly utilized by the heterotrophic organisms.

2.2.- RELATIVE ROLE OF ZOOPLANKTON AND BACTERIOPLANKTON

As for the section 2.1, in this discussion we will make use mainly of the results obtained for the zone 1S (1973-1975) and at the station "Ostend" (1977-1978).

Two major pieces of information were added:

2.2.1.-

On the one hand, at the level of the heterotrophic activity (*sensu stricto*) : as discussed earlier, a minimal value has been given. It reaches at least the same order of magnitude as the net primary production.

2.2.2.-

On the other hand, at the level of the grazing of the zooplankton on living phytoplankton (Daro, 1978). The results obtained with this method, where zooplankton is taking up radioactive phytoplankton, and the daily food requirement supply calculated on the basis of the weight of zooplankton are consistent and lead to the same kind of conclusion: the grazing by zooplankton concerns a low percentage of the phytoplankton biomass per day, even though the results may have been underestimated because most of the measurements were performed during day time.

These two pieces of information confirm earlier conclusions: the role of heterotrophic microorganisms is very important in the recycling of the produced organic matter, whereas the role of zooplankton is quantitatively much less important.

2.3.- COMPARISON BETWEEN THE THREE BIOCENOSES

In comparison with the ecological structure of the coastal marine system (station "Ostend") as it was discussed earlier, the following remark can be made about the two other stations (fig. 3 and 4).

2.3.1.-

Before discussing the quantitative differences, it has to be remembered that qualitative differences were noted.

The biochemical composition (proteins, carbohydrates and lipids) of the particulate organic matter, as well as of the phytoplankton and the primary production, is different in the three zones (Lancelot, in prep.).

At the level of zooplankton, such a difference was also noted, but it could be due to temporal variations linked with the development of the phytoplankton bloom (Hecq and Gaspar, in prep.) or to geographical variations.

2.3.2.- "Calais" (fig. 3)

2.3.2.1.-

The primary production measured at the station "Calais" is not significantly different from that of the station "Ostend". This conclusion is certainly not a definitive one, because of the small amount of measurements and because of the absence of any phytoplankton bloom at Calais during the sampling periods; it obviously needs to be confirmed during the following campaigns.

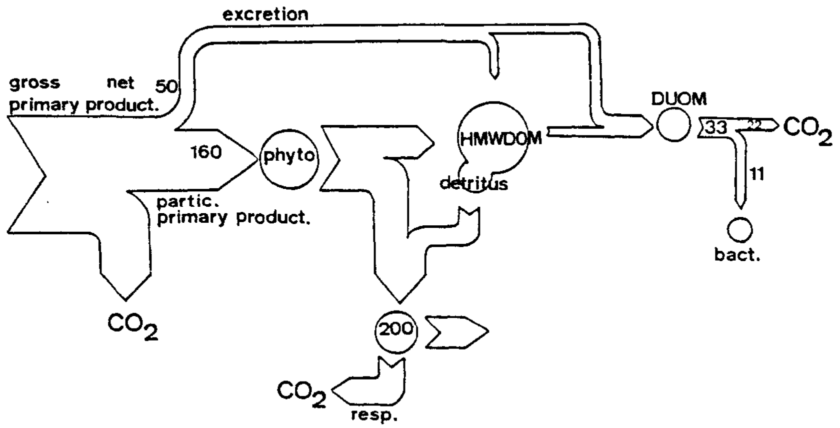

fig. 3.

Circulation of carbon between the first trophic levels at the station "Calais". (All fluxes in mg C/m^2 day.)

2.3.2.2.-

The heterotrophic activity (*sensu stricto*) is clearly lower than at Ostend, both in absolute value and in proportion to the primary production. This indicates that the bacteria here play only a minor role in the recycling of the produced organic matter.

2.3.2.3.-

The case of zooplankton is less clear. Zooplankton biomasses, expressed per m^2 are higher in Calais, but the measured grazing was very low: it seems even too low to allow the survival of the zooplankton present there. A possible interpretation is that the zooplankton preaccumulated fat reserves earlier in the season during a phytoplankton bloom, and was utilizing its own lipids during our sampling period (Hecq and Gaspar, in prep.).

A high value of zooplankton respiration could be used as a confirmation for this hypothesis.

New measurements are needed in order to confirm these observations and their interpretation.

2.3.2.4.-

The actual conclusion is that the recycling of organic matter is not made by heterotrophic organisms at Calais, as expected (see introduction). The complementary information on the importance of zooplankton has however still to be completed, before its relative role in the utilization of the primary producers is proved. So that, all in all, the results fit the hypothetical scheme of a proeminent role of zooplankton and the higher trophic levels at Calais, but they do not yet prove it definitively.

2.3.3.- "Hansweert" (fig. 4)

At Hansweert, a typical estuarian structure is found, with a very low primary production and high heterotrophic and respiratory activities. The situation is of course completely different from that at the other ecosystems, the exogenous organic matter here playing an important role.

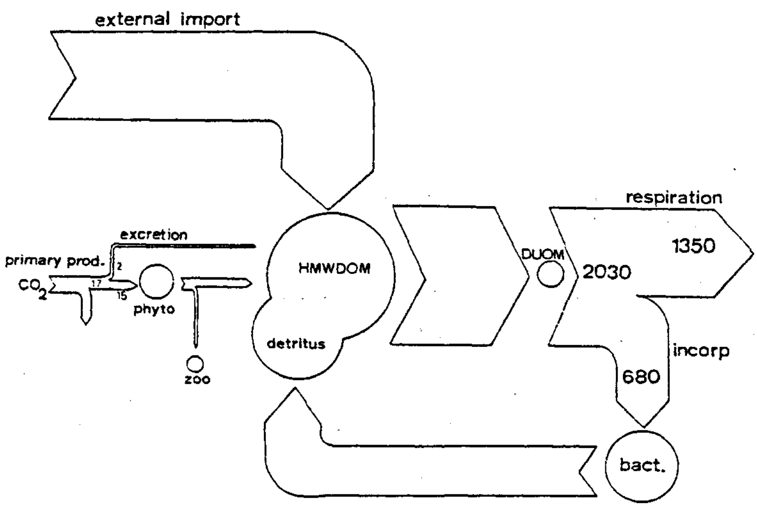

fig. 4.

Circulation of carbon between the first trophic levels at the station "Hansweert". (All fluxes in mg C/m^2 day.)

It is very interesting to note that, in those circumstances where phytoplankton activity is very low and can almost be neglected, the total respiration determined as oxygen consumption rate and the sensu stricto heterotrophic activity are not significantly different. This confirms that the measured heterotrophic activity is indeed the real one. No important element is missing and the differences noticed between total respiration and heterotrophic activity in the other zones can be attributed to a phytoplankton metabolism, such as phytoplankton respiration, as discussed earlier.

2.3.4.- Regulation of the circulation of organic matter at the first trophic levels

A proper understanding of trophic web structure and of its differences between the three zones investigated requires that the factors determining the intensity of each flux be known. This is particularly important at the sites of branching in the trophic web.

Three main branching determine the overall phytoplankton - zooplankton-bacteria bifurcation (fig. 5):

- the branching particulate/dissolved primary production
- the branching phytoplankton/zooplankton/detritus
- the branching detritus/zooplankton/bacteria.

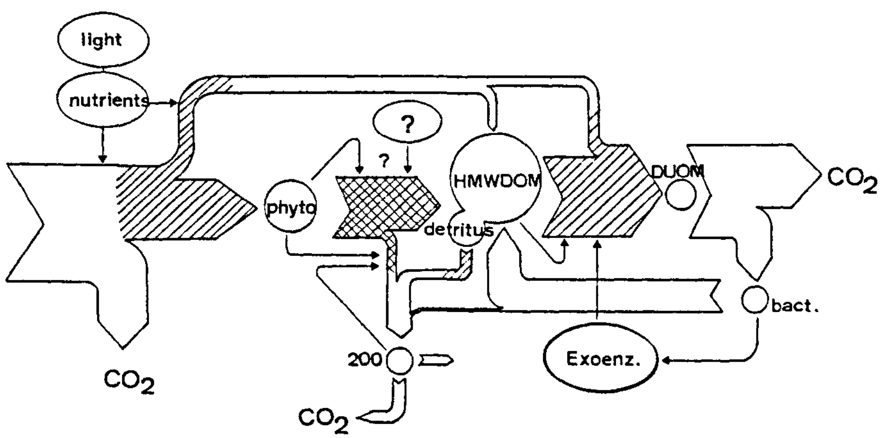

fig. 5.

Main regulation mechanisms of the carbon circulation between the first trophic levels in marine ecosystems.

2.3.4.1.- *The branching particulate/dissolved primary production*

According to the works of Anderson and Zeutschel (1970), Thomas (1971) and Berman & Holm-Hansen (1974) the phytoplankton excretion mainly results from an insufficient nutrient disponibility with the respect to photosynthetic carbon fixation. The relative value of dissolved versus particulate production would therefore be under the combined influences of light intensity and nutrient concentration.

The data obtained from our own measurements (Lancelot, submitted; Bertels, thesis work) are generally coherent with this theory (see Table 2).

Table 2

Seasonal variations of the phytoplankton extracellular release

	Date	Chlorophyll	% extracellular release
Ostend	050478[1]	16.2	22 %
	160478[2]	2.8	19 %
	190478[2]	4.8	31 %
	190478[1]	5	44 %
	160578[1]	5.9	60 %
Calais	040478[1]	3	19 %
	170478[2]	1.15	24 %
	180478[1]	0.84	23 %
	170578[1]	3.4	54 %
Hansweert	070478[1]	7.2	70 %
	210478[1]	6.3	0 %
	190578[1]	7.2	12 %

1. Lancelot (1979b).
2. A. Bertels (Thesis work).

- dissolved primary production is generally lower at Hansweert than at the other less eutrophic stations
- at Ostend and Calais, excretion increases during the course of the phytoplankton bloom, in parallel with the exhaustion of nutrients.

2.3.4.2.- *The branching phytoplankton/zooplankton/detritus*

Phytoplankton cells either are grazed by zooplankton or die and form detritus and dissolved organic matter.

The process of spontaneous phytoplankton mortality has now been widely recognized (Jassby and Goldman, 1974; Lund et al., 1958; Daro, 1974; Mommaerts, 1977). Its determinism, however, remains to be defined.

Grazing on living phytoplankton, on the other hand has been more closely investigated. It is dependant both on the quantity and on the quality (size and biochemical composition) of the phytoplankton present (Samain et al., 1975; Mayzaud and Poulet, 1978).

For the two main zooplanktonic species occuring during the spring bloom, namely *Temora longicornis* and *Pseudocalanus elongatus*, the form of the dependance of grazing on phytoplanktonic concentration has been experimentally put in evidence. The relationship is linear from 0 to 9-10 mg chlorophylla/ m^3. Above this value, grazing becomes independant of phytoplanktonic concentrations. This value being only very unfrequently reached, grazing is generally closely regulated by algal density.

On the other hand, the biochemical composition of phytoplankton and detritus (namely their relative content in proteins and carbohydrates) influences zooplankton grazing, growth and reproduction. Friedman & Sticker (1975) have demonstrated the existence of chemoreceptors allowing the copepods to select their food according to its nutritional quality.

Differences in this respect exist between the three biotopes we studied: phytoplankton cells synthetize relatively more proteins than carbohydrates in more eutrophic media (Ostend and Hansweert) than in oligotrophic ones (Calais).

Studies on the selectivity of grazing in relation to phytoplanktonic size and biochemical composition are in progress.

2.3.4.3.- *The branching detritus/zooplankton/bacteria*

As explained above, detritus and high molecular weigh dissolved organic matter (HMWDOM) can be ultimately degraded by bacteria only through the action of exoenzymes, hydrolyzing them into small organic polymers. These alone form the pool of directly usable organic matter (DUOM).

It may be surprising that, although the rate of heterotrophic bacterial activity differs by at least a factor of 10 between the three environments investigated (in the order Hansweert > Ostend > Calais), the size of this pool of DUOM is quite similar (table 3). It seems the overall rate of heterotrophic activity is not regulated by the pool size of its direct substrate.

This apparent paradoxe has been resolved by a simplified model developed by Billen et al. (submitted) showing that system formed by bacterial populations and their substrates produced at a rate P, rapidly reaches a stationnary state in which the size of the substrate only depends on the affinity of the bacteria for it, while only the size of the bacterial population and it total rate of activity depends on the production rate P.

The production of DUOM is the sum of direct excretion of small metabolites by phytoplankton and of exoenzymatic hydrolysis of detritus and HMWDOM. Very little is known about the kinetics of the action of free exoenzymes

Table 3

Concentration of small organic substrates determined at the at the three stations under study (in µmoles/ℓ)

	Ala	Asp	Lys	Glyc	Gluc	Acet	Lact
Hansweert							
mean	.049	.019	.013	3.6	0.07	1.1	0.2
max	.084	.033	.020	4.5	0.08	3.3	0.2
min	.020	.010	.010	2.0	0.05	0.2	0.2
Ostend							
mean	.029	.023	.020	2.6	0.03	1.0	1.7
max	.050	.030	.036	3.0	0.05	2.5	5
min	.010	.020	.010	1.8	0.02	0.2	0.2
Calais							
mean	.069	.037	.024	1.8	0.014	1.15	1.1
max	.176	.100	.034	2.3	0.040	4.0	1.6
min	.010	.010	.010	0.9	0.005	0.2	0.2

in natural waters, although their occurence has been demonstrated (Kim and Zobell, 1974; Reichardt et al., 1967).

Production of exoenzymes by bacteria has often been shown to be repressed by high concentration of monomeric organic substrates (Green and Colarusso, 1964; May and Elliot, 1968; Neumark and Citri, 1962; Hofsten, 1965). It is quite doubtfull, however, that such high concentration could ever occur in the water column, so that exoenzymes production is probably mostly dependant on bacterial density.

Khailov and Finenko (1970) have shown that the activity of exoenzymes is very dependant on the presence of particles on which macromolecules can adsorb.

Studies on the mechanisms of exoenzymatic degradation are in progress.

3.- Conclusion – Summary

All results actually available on the ecometabolism of the Southern Bight of the North Sea, i.e.:

- net primary production, particulate and dissolved;
- total planktonic respiration;
- heterotrophic activity (*sensu stricto*);
- grazing on living phytoplankton,

fit well together within the simple hypothesis that the respiration of the autotrophic organisms is much higher than estimated in the earlier calculations. The gross primary production would be much higher and the inconsistency between production and consumption would be solved in that way.

The comparison between the different biocenoses shows the existence of three different ecological structures:

- at Calais : an open sea situation. The phytoplanktonic production is not recycled mainly by heterotrophs (bacteria), but probably used by zooplankton and a complete food web;

- at Ostend : a typical marine coastal situation. The organic matter produced is mainly recycled by heterotrophic microorganisms (the bacterioplankton), after it has been made available to them by mortality and exoenzymatic hydrolysis. The role of zooplankton is much less important;

- at Hansweert : an estuarian situation. The high heterotrophic activity and total respiration are not dependant on a low primary production, but on important quantities of exogenous organic matter.

The research program for the next years will give a priority to more direct methods for the measurements of phytoplanktonic respiration and to the mechanisms of regulation of the branching from primary producers to zooplankton or to bacterioplankton.

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