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Ecometabolism of the coastal area
of the Southern Bight of the North Sea
Report of the workgroup "Organic Matter" (1979)

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Introduction

The study of the ecometabolism of any biotope requires

i) firstly, the identification of the main biological activities taking part in production and consumption of the organic matter and the stocks involved.

ii) secondly, the study of the main regulating mechanisms inducing a well balanced dynamic system.

The first point has already been developed in the coastal area of the Southern Bight of the North Sea (Billen *et al.*, 1976; Joiris *et al.*, 1979). However, as mentioned by these authors, some specific problems remained to be solved, and the "Organic Matter" workgroup has tried to do so by applying more refined methods for a better identification of the main biological activities and a proper understanding of the factors regulating the intensity of these activities.

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One important problem lies in the observation of a significant imbalance between the amount of organic matter produced by phytoplankton (main source of organic matter in area under study) and the amount of organic matter consumed, so that heterotrophic consumption was three times as high as production. In the absence of important exogeneous imports of organic matter, this had to be attributable to inadequate measures of phytoplankton gross production (underestimated ?) and/or heterotrophic consumption (overestimated ?). New methodologies were thus developed (Joiris et al., 1979) to obtain better measurements of all the fluxes involved in the gross phytoplankton production on the one hand and heterotrophic consumption on the other hand. The former includes phytoplankton particulate and dissolved production and phytoplankton respiration, the other, *sensu stricto* heterotrophic activity and phytoplankton respiration. Only this last parameter has not yet been measured. However new results lead to the hypothesis that phytoplankton respiration was more important than anticipated (Joiris et al., 1979). A method for measuring phytoplankton respiration had to be developed in order to verify this assumption.

Another important problem arising from the construction of the carbon budget concerned the recycling of the organic matter produced by phytoplankton. In contrast with the situation in the Northern Atlantic waters, where the recycling of phytoplankton production is classically accomplished by zooplankton (Daro, 1979), the recycling in the coastal area of the Southern North Sea presents the particularity of being accomplished almost exclusively by bacteria. The study of some regulatory mechanisms acting at sites of branching of the trophic web, decisive in the overall phytoplankton - zooplankton - bacteria - bifurcation was undertaken in order to understand this particular structure of the trophic web.

This work presents the last developments in the identification of the prevailing paths in the circulation of the organic carbon in the coastal area of the Southern Bight of the North Sea. An important part of this work will however be devoted to the description of some mechanisms of regulation, particularly important for the fate of the organic carbon produced by phytoplankton. This last point has needed larger ranges of concentrations and biological activities. Therefore, two other biotopes characteristic of the Southern Bight of the North Sea were sampled. A

richer one (station 'Hansweert' in the eutrophied Scheldt estuary) and a poorer one (station 'Calais' in the Channel). The position of the three sampled stations is indicated on fig. 1.

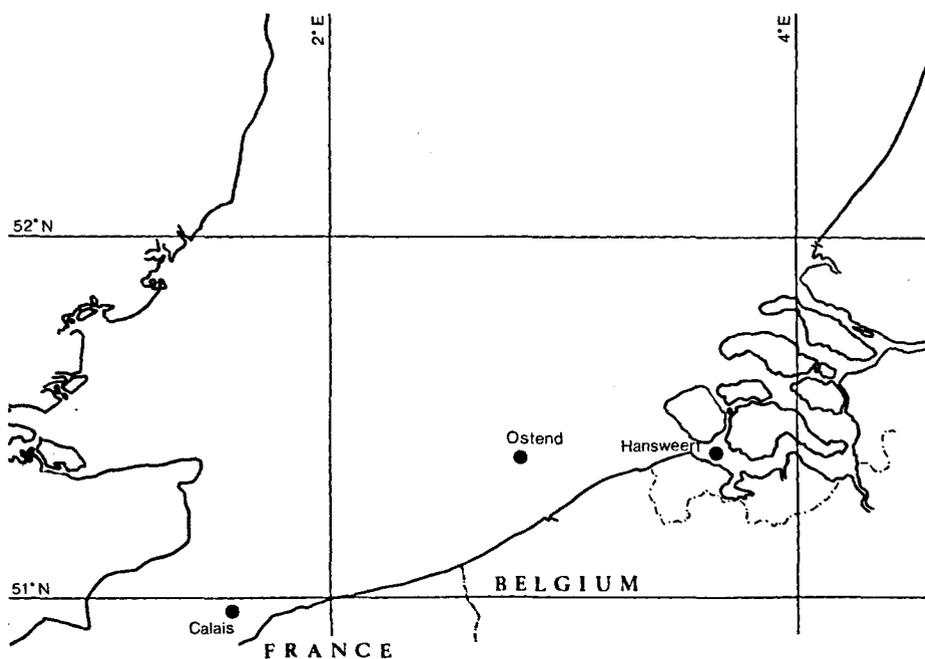


fig. 1.

Position of the sampling station visited

It must be still added that some other important results, more particularly concerned with the physiology and biochemistry of the plankton communities (phytoplankton, bacteria, zooplankton) were obtained during the cruises. Not directly useful for this work, they were discussed in separated papers (Billen *et al.*, 1980; Bossicart, 1980; Daro, 1980; Lancelot *et al.*, 1980).

Methods

The experimental part of this work was done on board of the *R. V. Mechelen* (coordinator : H. Picard).

Seawater was sampled at noon, at a depth of 3 m using Niskin's bottles. All the biological activities and stocks were measured on the same sample of seawater.

In addition to classical measurements of gross biological activities, new technical methods were developed to obtain a better understanding of the biological mechanisms. This was attempted by specifying the nature of the biological activities and the stocks involved. Two kinds of specification were studied, on basis of biochemical speciation and molecular weight fractionation, respectively.

1.- NET PHYTOPLANKTON PRODUCTION

Particulate and dissolved phytoplankton production were measured by the classical ^{14}C method of Steeman - Nielsen (1952).

However gross dissolved phytoplankton productions were measured kinetically in order to eliminate the negative effect of bacteria that can use some excreted products very fast (Nalewajko *et al.*, 1975; Lancelot, 1980).

Biochemical speciation of particulate primary production in proteins, carbohydrates and lipids was achieved through chemical fractionation of the radioactivity incorporated during incubation with H^{14}CO_3 after isotopic equilibrium (Morris *et al.*, 1974).

On the other hand, a first step to the biochemical speciation of the dissolved primary production was accomplished in separating the total excreted into small metabolites directly usable by heterotrophs and metabolites of high molecular weight. Ultrafiltration with membrane of 500 d porosity was applied on this experimental part (Lancelot, 1980, submitted).

2.- PHYTOPLANKTON DARK RESPIRATION

The method for measuring phytoplankton respiration was derived from the classical radiocarbon method of Steeman - Nielsen (1952). This flux was defined as the initial decrease of the radioactivity uniformly incorporated in phytoplankton cells when they are put into darkness.

Daily phytoplankton respiration was estimated assuming that the factors that quantitatively regulate respiration and particulate production are identical. This hypothesis still has to be verified.

3.- ZOOPLANKTON GRAZING

Grazing on living phytoplankton was determined by incubating zooplankton with pre-labelled natural phytoplankton populations and counting the radioactivity ingested (Daro, 1978). In addition, these experiments were done on 3 size class of phytoplankton cells in order to detect a possible size selectivity of the nutrition.

Grazing on detrital particles was estimated from the relative proportions of detritus and phytoplankton in the total particulate organic matter. This was done statistically from biochemical determinations of the total particulate organic matter (Lancelot-Van Beveren, 1980). Total grazing (on phytoplankton and on detritus), estimated in such way was in good agreement with the zooplankton grazing calculated from the population dynamic parameters determined by modelling (Bossicart and Mommaerts, 1979).

4.- TOTAL PLANKTONIC RESPIRATION

Total planktonic respiration was estimated by the classical measurement of initial dark oxygen consumption (Joiris, 1977).

5.- "SENSU STRICTO" HETEROTROPHIC ACTIVITY

Dissolved organic matter -the substrate of micro heterotrophs- involves a huge diversity of molecules about which little is actually known. According to Ogura (1975) and Billen *et al.* (1980), only a few are directly usable by heterotrophic bacteria.

This pool includes only small molecules (DUOM). The others must be first transformed to be usable by bacteria; for this reason they were called NDUDOM (non directly usable dissolved organic matter).

"Sensu stricto" heterotrophic activity was then defined as the rate of utilization of the small DUOM molecules. The method for determining it consists of measuring the uptake kinetics of ^{14}C labelled organic molecules with high specific activity (Billen *et al.*, 1980).

Results and discussion

1.- GENERAL PICTURE OF THE ECOSYSTEM

Figure 2 shows the circulation of organic carbon at the first trophic levels in the coastal area of the Southern Bight of the North Sea during the spring phytoplankton bloom (March to July).

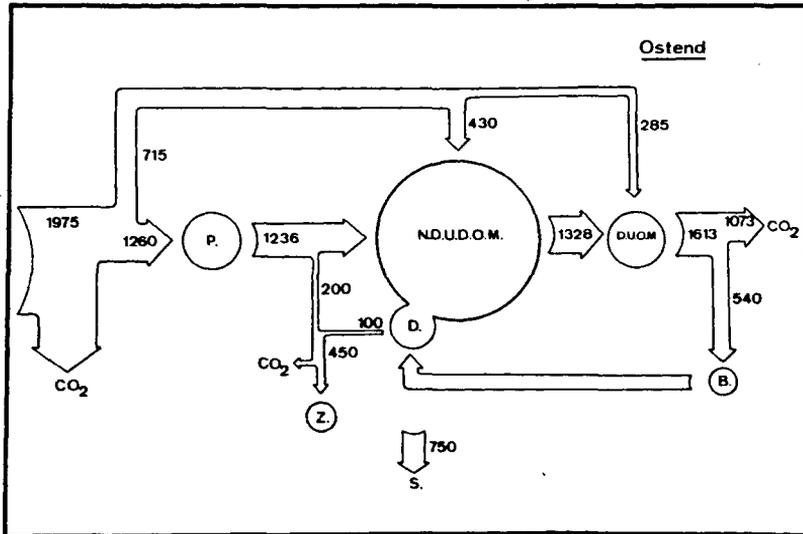


fig. 2.

Circulation of carbon budget ($\text{mg C/m}^2\cdot\text{day}$) between the first trophic levels at the station 'Ostend' (period March - July).

Abbreviation :

P : phytoplankton Z : zooplankton S : sediments
 B : bacteria D : detritus
 ND.U.D.O.M. : non directly usable dissolved organic matter
 DUOM : directly usable organic matter

Some remarks can be made from this figure, namely:

- The direct production of DUOM by phytoplankton is not very important (14% of the net phytoplankton production).

Moreover it contributes to only 17% of the total *sensu stricto* heterotrophic activity whose substrates appear to be chiefly sup-

plied by hydrolysis of the degradation products of died phytoplankton cells.

- Recycling of the organic carbon produced by phytoplankton is mainly attributable to heterotrophic microorganisms. This confirms the idea of a minor role of zooplankton in the recycling of organic carbon produced by phytoplankton in the coastal area of the Southern Bight of the North Sea (Billen *et al.*, 1976; Joiris *et al.*, 1979).
- Phytoplankton respiration appears to be more important than generally estimated in marine waters (Steeman-Nielsen and Hansen, 1959). Its contribution to the total planktonic respiration is greater than *sensu stricto* heterotrophic activity it self.

However the carbon budget (Table 1) shows a little discrepancy between the measured total planktonic respiration and the sum of *sensu stricto* heterotrophic activity and phytoplankton respiration, the two components of the total planktonic respiration.

Table 1

Carbon budget at the station Ostend (period March-July) in mg C/m².day

Net phytoplankton production	1 975	Heterotrophic activities	1 913
particulate	1 260	<i>Sensu stricto</i>	1 613
dissolved	715	Zooplankton grazing	300
Phytoplankton respiration	1 930	Total planktonic respiration	5 500
Gross phytoplankton production	3 905	Phytoplankton respiration	1 930

Some observations still lead to the conclusion that the contradiction should be attributable to underestimated values of phytoplankton respiration caused by the lack of correct daily values, *i.e.*

i) the budget of net phytoplankton production and heterotrophic activities (*sensu stricto* and zooplankton grazing) are well balanced.

ii) the comparison with the same measurements accomplished in Hansweert, a biotope where the contribution of phytoplankton to the pool of organic matter is minor compared to the terrigenous imports (Wollast, 1976; Joiris *et al.*, 1979) indicates that phytoplankton respiration contributes effectively to less than 20% of the total planktonic respiration (fig. 3).

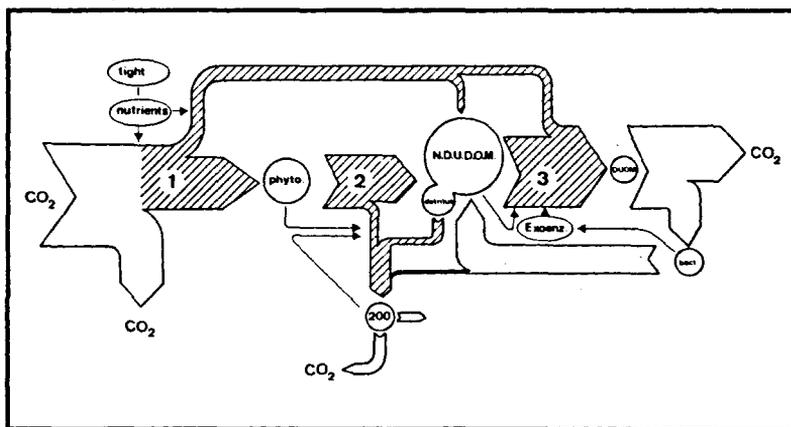


fig. 4.

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

2.1.- REGULATION OF THE RELATIVE PROPORTIONS OF PARTICULATE AND DISSOLVED PHYTOPLANKTON PRODUCTION

The relative value of dissolved versus particulate production is known to be influenced by both, the light intensity and the available nutrients (Fogg *et al.*, 1965; Hellebust, 1965; Nalewajko, 1966; Anderson and Zeutschel 1970; Thomas, 1971 and Berman and Holm - Hansen, 1974).

No light intensity effect could be detected from our own experiments. However, the percentage of phytoplankton extracellular release (P.E.R.) was found to be entirely dependent on the disponsibility of dissolved mineral nitrogen. Two kinds of observations have led to this conclusion.

2.1.1.- Geographical variations

Geographical variations show that the richer a biotope, the weaker P.E.R. (Table 2).

Table 2

Mean P.E.R. in the three biotopes

Biotopes	P.E.R.	Ranges of nitrogen ($\mu\text{mole/l}$)
Calais	50 %	2 - 16
Oostende	40 %	8 - 28
Hansweert	15 %	300 - 450

2.1.2.- Seasonal variations

Seasonal variations show, for each studied biotope, a linear increase of P.E.R. with the decrease of available dissolved nitrogen (fig. 5). This means that when nitrogen becomes scarce but light is still sufficient, a greater part of photosynthetically fixed carbon is excreted in the surrounding medium by phytoplankton cells. This suggests that environmental conditions which inhibit cell multiplication but still allow photo-assimilation to continue, result in the release of higher proportions of photoassimilated carbon.

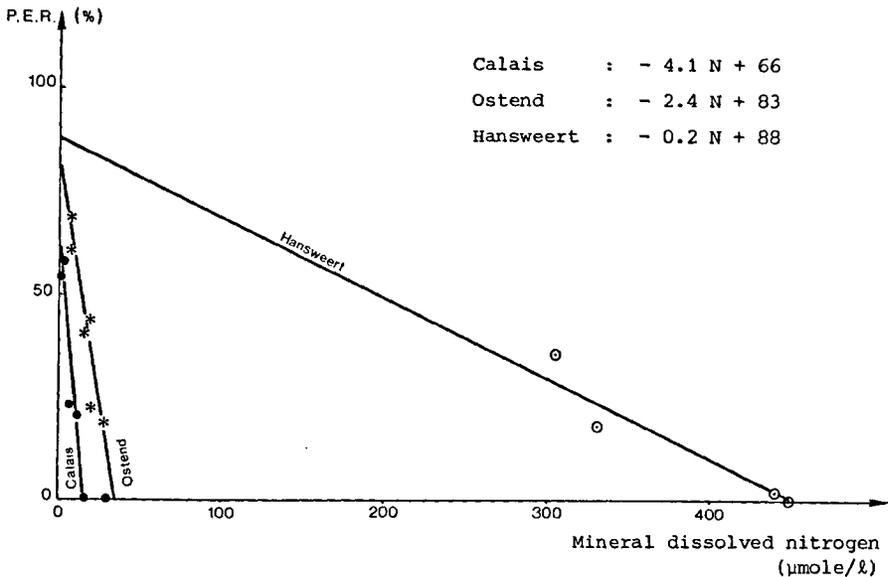


fig. 5.

Seasonal variations of the percentage extracellular release (P.E.R.) by phytoplankton in three biotopes characteristic of the Southern North Sea.

Results show in addition that the physiological response of phytoplankton cells to nutritional changes in the external medium appears to be specific to each biotope.

2.2.- REGULATION AT THE LEVEL OF THE BRANCHING

phytoplankton $\begin{cases} \rightarrow \text{detritus} \\ \rightarrow \text{zooplankton} \end{cases}$

Phytoplankton cells produced during the spring can either be ingested by zooplankton organisms, either die and supply the pool of particulate and dissolved detrital matter.

Natural mortality was estimated to be about 80 % of the particulate production during spring. Reasons of this mortality (physiological stress, senescence...) are not known up to now.

On the other hand two factors mainly operate on the regulation of zooplankton grazing on phytoplankton cells, namely:

- the frequency of nutritional activities
- the dietetical qualities of some classes of phytoplankton cells whose dimensions do correspond to the filtration capacity of zooplankton organisms.

2.2.1.- Frequency of nutritional activities of zooplankton

A few day-and-night experiments of zooplankton grazing indicate a great variation in zooplankton feeding activities, partly attributable to vertical migrations (fig. 6).

Integrated daily and nightly measurements of grazing indicate that the latter is in general more important than the former (Table 3). However this phenomenon is not established but on some occasions, the night value can be 7 times the day value.

Study of the regulation of this phenomenon is in progress.

Table 3

Daily and nightly grazing of zooplankton

Biotope	Sample	Daily grazing µg chl. a/m ²	Nightly grazing µg chl. a/m ²
Oostende	01-04-78	142	275
	09-04-78	310	380
	10-04-78		1 227
	13-04-78	520	1 080
	16-04-78	181	180
	Calais	03-04-78	10
04-04-78		22	32
07-04-78		25	32
11-04-78		13	95
17-04-78		16	39

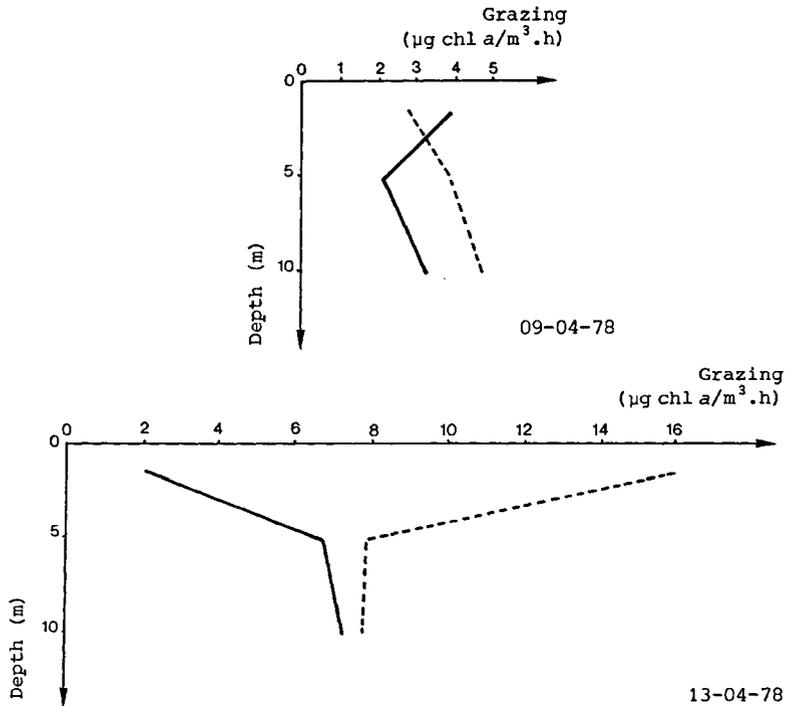


fig. 6.

Day-night vertical distribution of zooplankton grazing
 0 h : broken line 12 h : continuous line

2.2.2.- *Dietetical qualities of phytoplankton cells*

Zooplankton feeding activities are known to be dependent on the quantity and quality (size and biochemical composition) of phytoplankton cells (Boucher et al., 1975; Friedman and Strickler, 1975; Hargrave and Geen, 1970; Mayzaud and Poulet, 1978). Two aspects of the incidence of biochemical composition of phytoplankton cells on zooplankton feeding activities were studied :

- i) the seasonal variations of the biochemical composition of phytoplankton cells, its distribution among different size classes and its regulation.
- ii) the natural selectivity of zooplankton grazing in some size classes of phytoplankton cells.

i) The biochemical characterization of phytoplankton includes the determination of proteins, carbohydrates and lipids, the necessary metabolites of zooplankton growth.

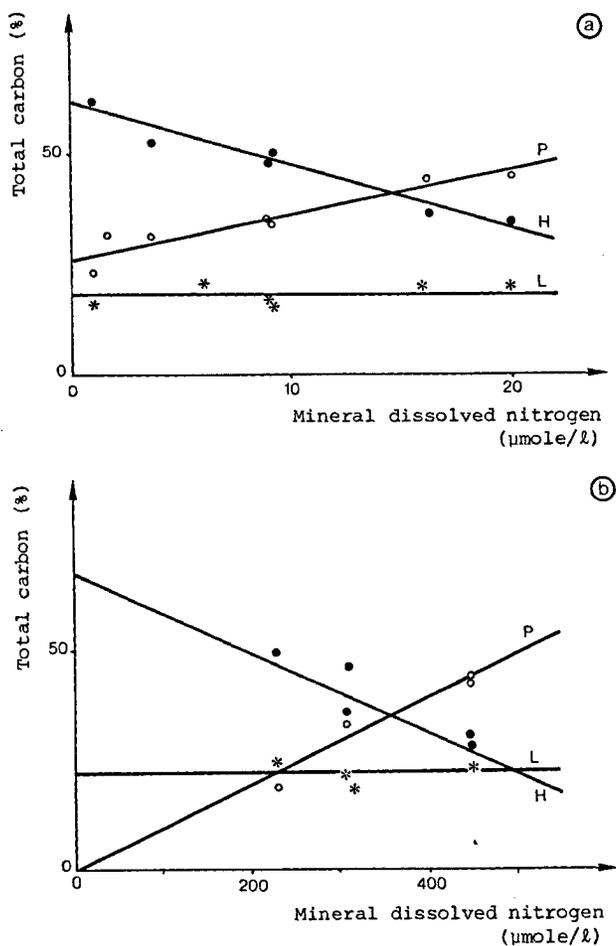


fig. 7

Variations of the percentage of proteins, carbohydrates and lipids in phytoplankton cells in function of the availability of the dissolved mineral nitrogen

(a) Marine biotopes

(b) Estuarine biotopes

The seasonal variations of the phytoplankton productions of proteins, carbohydrates and lipids indicate that the biochemical composition of phytoplankton cells is regulated by the availability of dissolved mineral nitrogen in marine and estuarine biotopes (fig. 7). The decrease of dissolved mineral nitrogen in the course of the spring bloom leads to the linear decrease of the amount of proteins at the benefit of polysaccharides.

Table 4

Percentage of β 1-4 glucan of phytoplankton cells (Ostend)

Samples	β 1-4 glucan	
	% total carbohydrate	% biochemical carbon
02-04-79	18	5
03-05-79	39	22
21-05-79	56	34

The simultaneous increase of the reserve polysaccharide β 1-4 glucan (Table 4) among the carbohydrates indicate the constitution of storage products during the decay of the bloom. The steadiness of the lipids during the bloom shows in addition that lipids do not constitute reserve products for phytoplankton in the Southern North Sea.

In addition, seasonal variations of the biochemical composition lead to the succession of phytoplankton cells of different size classes (fig. 8), characterized however by a similar mean biochemical composition (Table 5).

Table 5

Part of proteins, carbohydrates and lipids among three size classes of phytoplankton cells in Ostend

Metabolite	Size classes of phytoplankton cells		
	< 25 μ	> 25 μ < 100 μ	> 100 μ
Proteins	38 %	43 %	38 %
Carbohydrates	43 %	35 %	50 %
Lipids	19 %	20 %	12 %

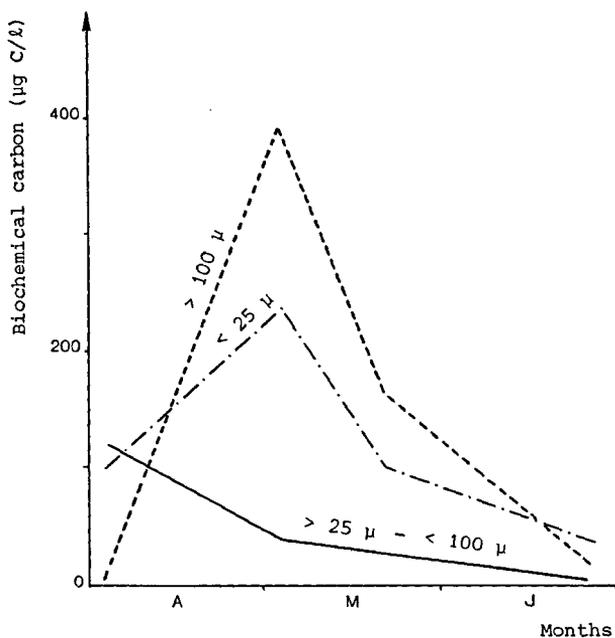


fig. 8.

Distribution of the biochemical carbon
in three sizes of phytoplankton cells.

ii) Moreover, experiments of zooplankton grazing on these three sizes of phytoplankton cells suggest a natural selectivity in the choice of phytoplankton particles (fig. 9). The dominant zooplankton species of spring, *Temora*, ingests preferably phytoplankton particles whose size ranges between 25μ and 100μ (up to 80 %). These particles correspond unfortunately to the less abundant class of phytoplankton cells (fig. 8) occurring during spring. Indeed the dominant phytoplankton species of spring includes small flagellates, alone ($< 25 \mu$) or aggregated ($> 100 \mu$). The former are too small for the filter-feeder, the latter too big. Consequently, the numerous phytoplankton cells produced during spring cannot be grazed by zooplankton. Set in the poor nutritive conditions of the end of the bloom, these phytoplankton cells die and increase the pool of detrital organic matter.

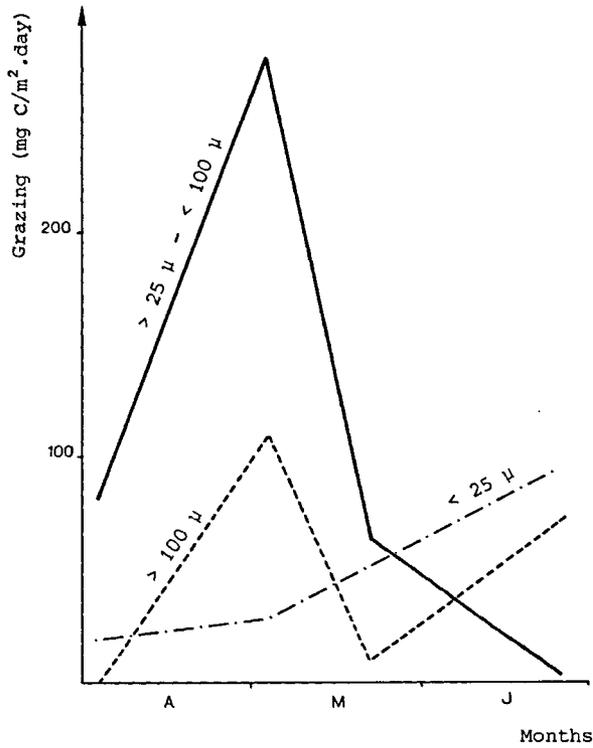
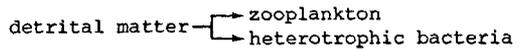


fig. 9.
Selectivity of zooplankton grazing in the choice of three sizes of phytoplankton cells

2.3.- REGULATION AT THE LEVEL OF BRANCHING



Detrital matter arises mainly from dead organisms belonging to originating from the trophic web in the coastal area of the Southern Bight of the North Sea. Particulate and dissolved detritus are both to be found in the surrounding medium.

Particulate matter can be ingested by zooplankton organisms and other particle feeders. However it must be first hydrolysed into small metabolites to be taken up by bacteria.

2.3.1.- Detrital matter → zooplankton

i) A first reasonable approximation consists in considering that the selectivity criterium of zooplankton for detritus must be related as for phytoplankton cells to the size of detrital particles. Regulation of their intake by zooplankton will depend on the production of detrital particles of adequate dimensions. This interaction is thus mainly under control of phytoplankton which checks the quantity and quality of detrital organic matter in the coastal area of the Southern North Sea (Lancelot - Van Beveren, 1980).

ii) On the other hand, some preliminary experiments seem to assume that dissolved detrital organic matter is never intaken by zooplankton even when phytoplankton cells are scarce (Hecq, 1979).

2.3.2.- Dissolved organic matter → bacteria

i) Description of the pool of dissolved organic matter

The pool of dissolved organic matter includes a huge diversity of organic molecules among which some are directly usable by micro-heterotrophs (DUOM); some among the others (NDUDOM) can become usable by means of some chemical transformations.

The comparative study of initial rates of organic matter consumption (v_i , table 6) measured on total dissolved organic matter and the pool of small metabolites (M.W. < 500 d) isolated by ultrafiltration shows that the low molecular weight fraction accounts for most of the directly usable organic matter (DUOM). Part of that pool evidently includes free amino

Table 6

Comparison between concentration and biological usability
of organic matter before and after ultrafiltration
(molecular weight < 500 d)

Samples	Total organic carbon (mg C/l)	Total carbohydrates (mg C/l)	BOD ₅ (mg C/l)	v_i (mg C/l)
Calais				
seawater	6	1.7	0.6	-
< 500 d	11	0.5	0.5	-
Ostend				
seawater	15	1.9	0.8	0.024
< 500 d	22	1	0.5	0.026

acids and their small oligomers, monosaccharides and small oligosaccharides, ..., as previously shown (Billen et al., 1980). Moreover, the comparison of BOD₅ and TOC measurements (and even carbohydrates analyses) indicates that an important part of the low molecular weight substances are not quickly used by micro-heterotrophs.

The pool NDUOM on the other hand, probably includes in addition to the small metabolites non directly usable, biological polymers that must be first converted into small substrates to be usable by bacteria. Part of the pool appears however to be refractory to any degradation and will compose fossil organic matter. Some, on the other hand, will be hydrolysed into small metabolites. Preliminary experiments (Table 6) seem to indicate that this degradation would be however very slow (more than 5 days).

ii) Which mechanisms will determine the intensity of the degradation of dissolved organic matter? Two possible aspects have been examined in this study:

a. A direct method has been used in order to test the biodegradability of macromolecules, by following the effect of their addition on the oxygen consumption as a function of the time. First results are presented in table 7. They show the usability of starch within a few days. In the case of cellulose the utilization is much more slower and proceeds at a rate which seems independent of the amount added.

Table 7
Test of biodegradability of added macromolecules
in natural seawater

Day	Addition (mg C/l)				
	Starch		Cellulose		
	0.5	5	0.5	0.3	3
1	0.00	0.04	0.01	0.11	0.11
5	0.22	0.43	0.28	-	-
6	-	-	-	0.24	0.36
10	0.22	0.15	0.57	0.27	0.48
15	-	-	-	0.33	0.83

b. Exoenzymatic activity of natural seawater. Labelled high molecular weight proteins and carbohydrates obtained from a phytoplankton culture

have been added to natural seawater filtered on a 0.22 μ pore size filter, and to artificial seawater. The study of the appearance in the medium of labelled low molecular weight substances revealed an exoenzymatic hydrolysing activity of the natural seawater (for detailed data, see Billen *et al.*, 1980 b).

Conclusions

The picture of the trophic web of the coastal area of the Southern Bight of the North Sea has outlined two important particularities if compared with classical trophic webs. Namely:

- an important contribution of phytoplankton respiration (more than 50 %) to total planktonic respiration.
- a minor role of zooplankton organisms in the recycling of the organic matter produced by phytoplankton.

The study of some important regulatory mechanisms directly involved in the destiny of the carbon produced by phytoplankton has carried some explanations about the working of this ecosystem.

The minor role of zooplankton in the recycling of organic matter produced by phytoplankton is mostly attributable to the inadequacy of the size of phytoplankton cells. From then nutritional qualities of phytoplankton cells seem not to be decisive in the feeding activities of zooplankton although these nutritional qualities are not equivalent during the phytoplankton bloom. Indeed the physiology of phytoplankton cells appears to be controlled by the availability of dissolved mineral nitrogen. The lack in this essential nutrient lead to a shift in the destiny of the photo-assimilated carbon. Higher quantities of reserve polysaccharides and extracellular metabolites will be built when nitrogen becomes scarce. These last metabolites contribute directly to the supply of the pool of dissolved organic matter, substrate of heterotrophic bacteria.

However the carbon budget has shown that this pool is mainly supplied by degraded phytoplankton cells.

Among the huge diversity of molecules involved in this pool, a very little part is however directly usable by heterotrophs (DUOM). The others (NDUDOM) must first be converted into substrate DUOM to be usable by heterotrophs.

Some preliminary tests have shown that the transformation of substrat NDUDOM into DUOM would be very slow probably because more than one mechanism is involved in this chemical transformation. Among these, the action of exoenzymes should be taken into account.

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