THÜNEN
Digitalization sponsored
by Thünen-Institut

C.M. 1982/L:31
Biological Oceanography Committee

This paper not to be cited without prior reference to the authors

Part 1

GENERAL STRUCTURE OF THE ECOSYSTEM

J.M. BOUQUEGNEAU[1], G. BILLEN[2], C. JOIRIS[3], M.H. DARO[3], C. LANCELOT[2],
J.H. HECQ[4], A. BERTELS[3], M. BOSSICART[3], M. SOMVILLE[2], J.P. MOMMAERTS[5],
J. WIJNANT[3] and J.C. WEHREN[1]

Studies by the workgroup "Organic matter" are concerned with the description and the understanding of the carbon cycling in the Southern Bight of the North Sea, and more particularly in the zone 1S which includes the belgian coastal zone.

This ecosystem is defined on a hydrological basis (fig.1), the zone being dominated by the residual current entering from the Channel and directed to the North-East. The presence of the Scheldt estuary, however, seems to induce a gyre in front of the Belgian coast, where the freshwater from the Scheldt resides for some times (Nihoul & Ronday, 1975). On basis of this general circulation pattern, the Belgian coastal zone is defined as the region in front of Zeeland and Belgium limited by a current velocity of 200.10^3 $m^3.s^{-1}$ (fig.1). This zone extends to about 40 km offshore over an area of 5.370 km^2, has a mean depth of 15m and is strongly influenced by terrestrial inputs from the Scheldt, the derivation channel of the Lys and the river Yser. Salinity is generally less than 33 ‰. Turbidity is generally high, with mean values above 5 $mg.l^{-1}$ and maxima of 15 $mg.l^{-1}$ (Moens, 1974).

1. Laboratoire d'Océanologie, Université de Liège.
2. Laboratoire d'Océanographie, Université libre de Bruxelles.
3. Laboratorium voor Ekologie en Systematiek, Vrije Universiteit Brussel.
4. Laboratoire de Biologie marine, Université de Liège.
5. Unité de Gestion du Modèle mathématique de la mer du Nord et de l'estuaire de l'Escaut, Ministère de la Santé publique.

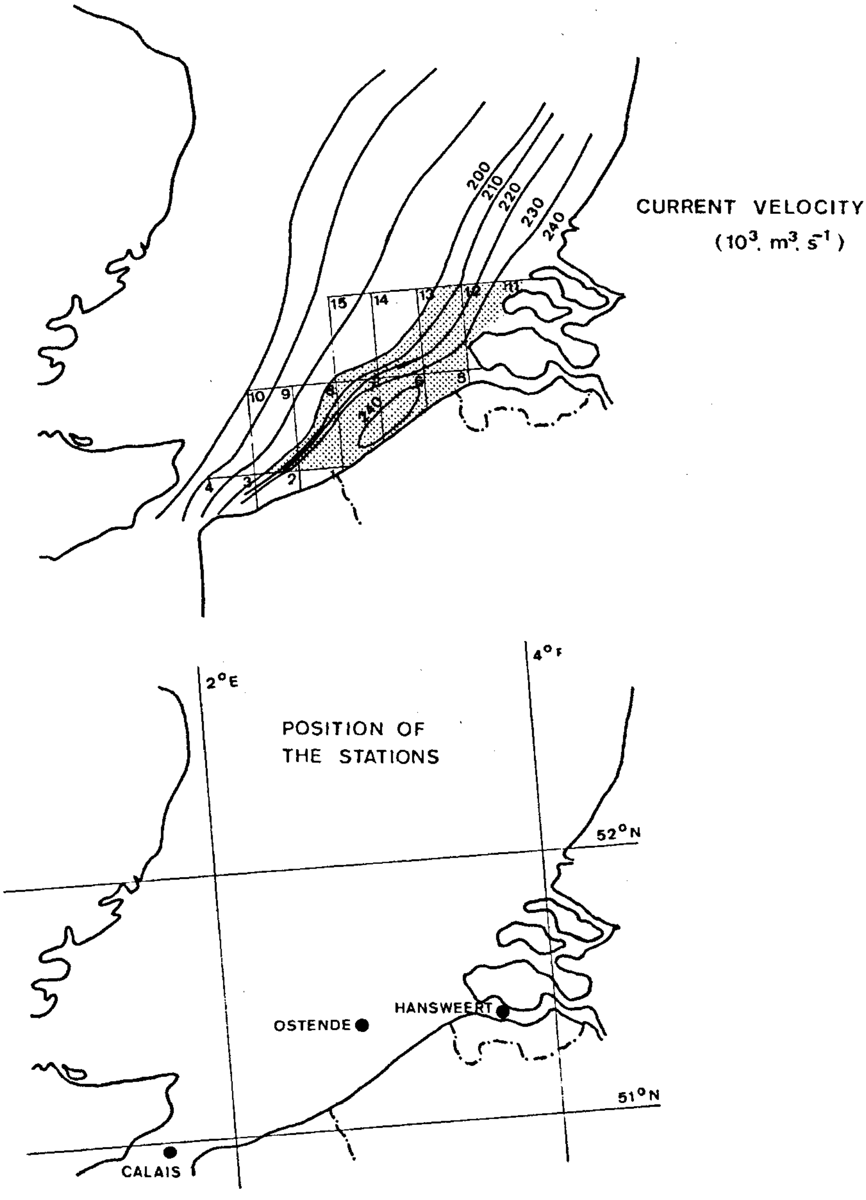

Fig. 1 : Position of the stations.

The grid points used for establishing the mathematical model of the North Sea have been investigated. However, "Ostend" and "Westhinder" stations have been considered to be representative of the belgian coastal zone and have been more carefully sampled (fig.1).

Moreover, in order to understand the effects of terrestrial inputs on the ecosystem, four other stations have been considered : stations "Calais" and "Boulogne", waters with "atlantic" characteristics in the English Channel ; station "Hansweert", highly eutrophied water of the Scheldt estuary (35 km from the open sea) and the Fladdenground (Northern atlantic water).

The ecometabolism of the zone 1S (Ostende-Westhinder) will be first described and secondly, it will be compared to other stations.

1° The carbon cycling in the zone 1S

The general picture of the mean annual carbon standing stocks and fluxes of the ecosystem is described in fig.2. We will examine the successive compartments of the ecosystem with their spatial and seasonal variations, each of them (except inorganic carbon) beeing otherwise more precisely studied in the following chapters of this work.

a. Inorganic carbon

Inorganic carbon concentration has been estimated to be 390g C/m^2. Carbonated alkalinity is about 2.35 mM and the mean pH of the zone is about 8.4 (note that it is more acidic just near the shore). The partial pressure of CO_2 calculated from these data is about 210 μatm, which suggests an input from air of about 60g $C/m^2.y^{-1}$ calculated on the basis of the rate constant of transfer of CO_2 through the air-sea interface of Sugiura et al (1963) (0.007 $m.mol.cm^{-2}atm^{-1}min^{-1}$). This input controls

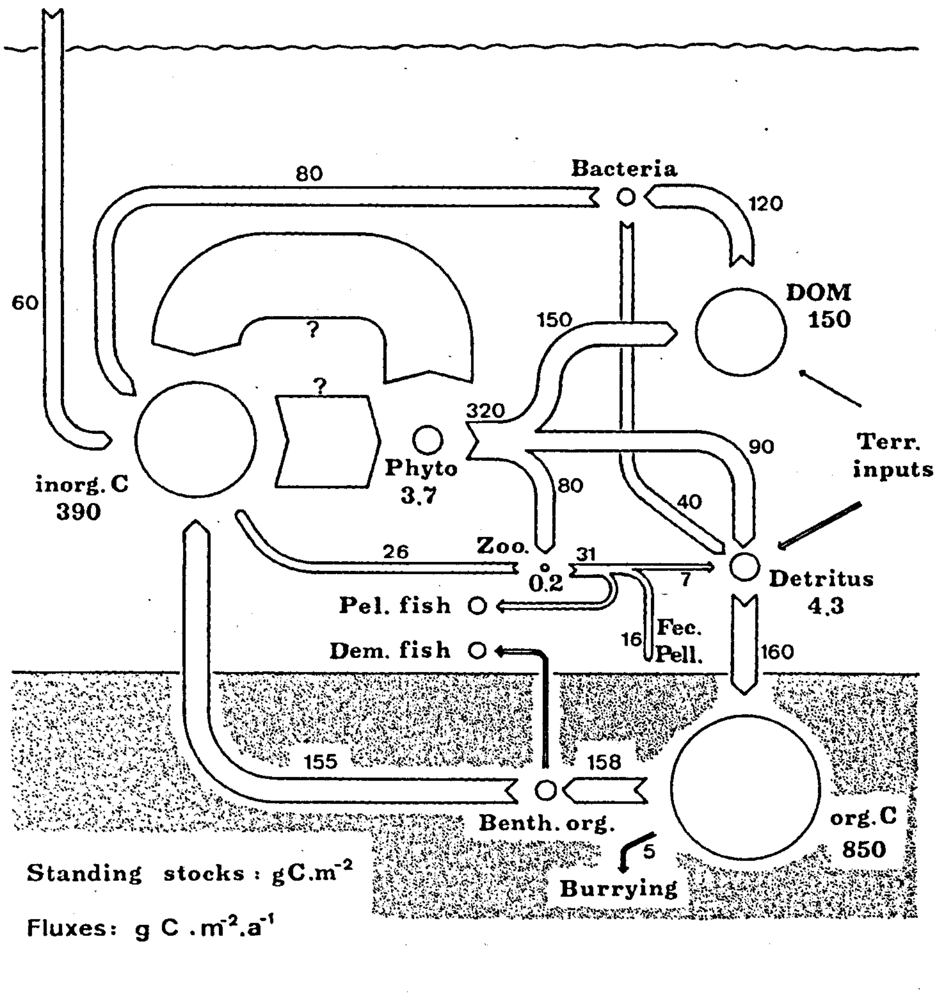

Fig.2 : Mean annual carbon standing stocks and fluxes in the zone 1S of the Southern Bight of the North Sea.

the inorganic carbon decrease resulting from the fact that net photosynthesis (320g $C.m^{-2}.y^{-1}$) is greater than the non-phytoplanctonic global respiration in the ecosystem (155 + 80 + 26g $C.m^{-2}.y^{-1}$). However, pH shows nycthemeral variations due either to diurnal photosynthetic and respiration activities and nocturnal respiration activity or to the water movements of the tides (fig.3).

b. Primary production

The phytoplankton biomass as well as bacteria and detritus are determined by measuring the chlorophyll a and the total particulate organic carbon (Σ proteins, carbohydrates and lipids). The part of the organic carbon content of phytoplanktonic cells was estimated from the chlorophyll a concentrations, using a C-organic/chlor.a ratio own to each season. These specific ratios were determined by the linear regression of organic carbon on chlorophyll a, both measured on the total particulate organic matter (Lancelot-Van Beveren, 1980).

Chlorophyll a concentrations show a decrease from the shore to sea and from the Scheldt estuary to the French border (fig.4). This gradient is particularly sharp in the spring, when concentrations in the coastal zone are at least one order of magnitude higher than in the offshore zone.

Potential primary production, expressed per unit water volume, follows the same distribution as chlorophyll, but as the coastal water is more turbid, the photic layer is much shallower there (about 5m) than in open sea (up to 25m), so that the integrated primary production is rather uniform in the whole zone (Mommaerts, 1973b). The phytoplanktonic communities are however different in the coastal and the offshore zone : the ratio net-/nannoplankton in primary production shows a prominent role of netplankton nearshore and micro-flagellates offshore, during the spring bloom (Mommaerts, 1973a). Netplankton cannot be too strickly assimilated to diatoms, because it is largely dominated by the colony forming micro-flagellate *Phaeocystis pouchetii* during the spring bloom.

Chlorophyll measurements (fig.5a), estimations of phytoplankton biomass and of detritus concentrations (fig.5b), obtained during several years in the area show a clear spring bloom, during the second half of April and the beginning of May, immediately followed by a peak in detritus. An autumn bloom was sometimes detected, but not found each year. Particulate primary production measurements (fig.5c) again show a clear spring bloom now lasting from mid-March to June, while no second bloom clearly appears - but the existence of an August bloom, sometimes detected in an adjacent area, cannot be excluded. In situ and semi-situ measurements of dissolved primary production show a relation-

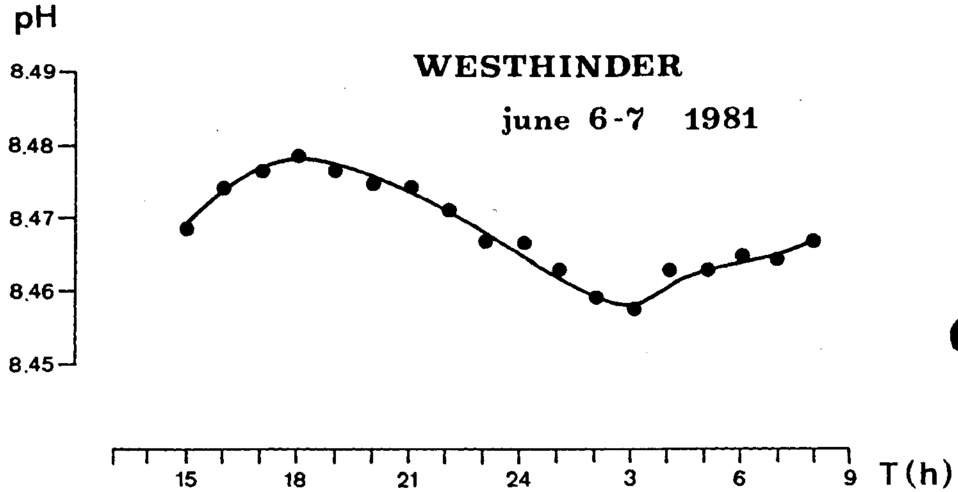

Fig.3 : Nycthemeral variation of pH

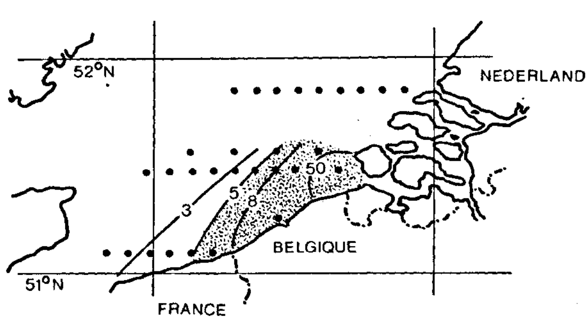

Fig.4 : Distribution of chlorophyll a

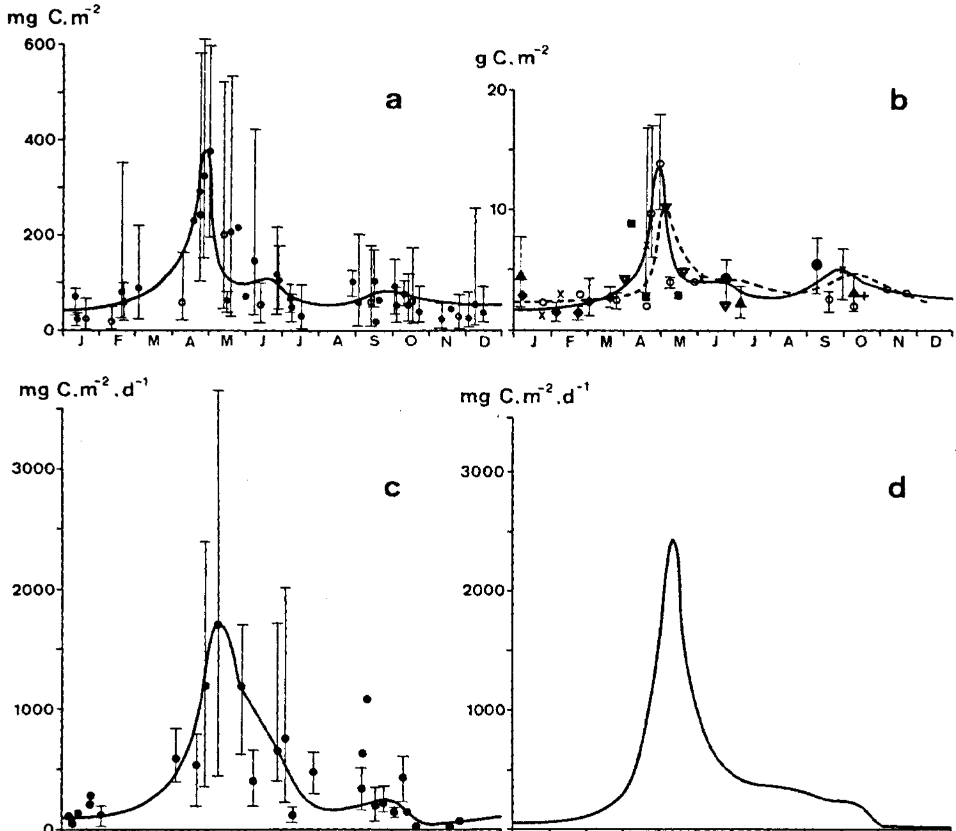

Fig.5 : Annual variations of chlorophyll a concentrations (a), phytoplankton biomass (b,—), detritus concentrations (b,--), particulate (c) and dissolved (d) primary production.

ship between extracellular release, expressed as a percentage of the total primary production, and the concentration of mineral nitrogen : excretion decreases with increasing nitrogen concentration (fig.6). This empirical relation was used for calculating the curve of seasonal evolution of dissolved primary production (fig.5d).

The gross primary production however reveals uneasy to be estimated. Indeed, whilst it is generally accepted that the phytoplanktonic respiration should be about 50% of the gross primary production, the loosing of labelled CO_2 by phytoplankton in the dark suggests that phytoplanktonic respiration is very high (about 10% of the biomass/hour)(fig.7). Moreover, the measurements of the nycthemeral variations of oxygen, CO_2 and particulate carbon concentrations in the water column suggest gross primary production and phytoplanktonic respiration much higher than expected. However, it is necessary to point out the fact that till now it has not been possible to differentiate the part of the variations resulting from the nycthemeral variations of the biological activities and from the water movements of the tides.

Whatever the case, the estimation of the phytoplanktonic respiration does not affect the general picture of the carbon cycle since only the net primary production is used in the food web. The mean annual phytoplankton biomass has been estimated to be 3.7g C/m^2 and the net primary production 320g $C/m^2.y^1$.

The fate of the net primary production is threefold :

1° the dissolved production (150g $C.m^{-2}.y^{-1}$) contributes to the enrichment of the pool of <u>dissolved organic matter</u> (see part c of this chapter and chapter IV of this work).

2° one part of the net particulate primary production (80g $C.m^{-2}.y^{-1}$) is grazed by <u>zooplankton</u> (see part d of this chapter and chapter III of this work).

3° the ungrazed part of the net particulate primary production (90g $C.m^{-2}.y^{-1}$) contributes to the enrichment of the pool of <u>detritus</u> which are recycled by benthic organisms (see part e of this chapter and chapter IV of this work).

c. The dissolved organic matter and its utilization by planktonic microheterotrophs

The total dissolved organic carbon concentration is quite important (150g $C.m^{-2}$) but a large part of this pool seems to be unused by bacteria. Indeed, the BOD_5 is only 15g.C/m^2, i.e. 10% of the total, and the directly usable substrates of low molecular weight account for 2g $C.m^{-2}$. Exoenzymatic hydrolysis of macromolecules is therefore required to explain the heterotrophic activity (see chapter IV). However, it is worth noticing that previously carried out experiments about the comparative study of initial rates of organic matter consumption measured on total dissolved organic matter and the pool of small metabolites suggests that the low molecular weight fraction could account for most of the directly usable organic matter and that a part of that low

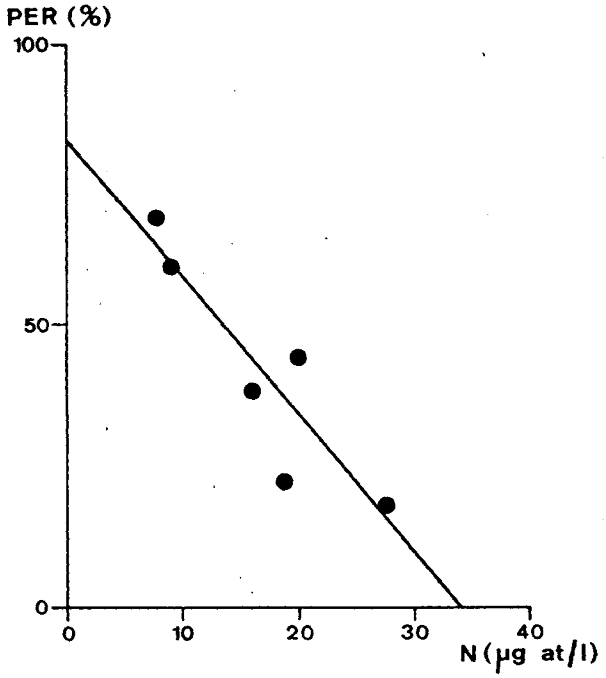

Fig.6 : Relationship between extracellular release and concentration of mineral nitrogen.

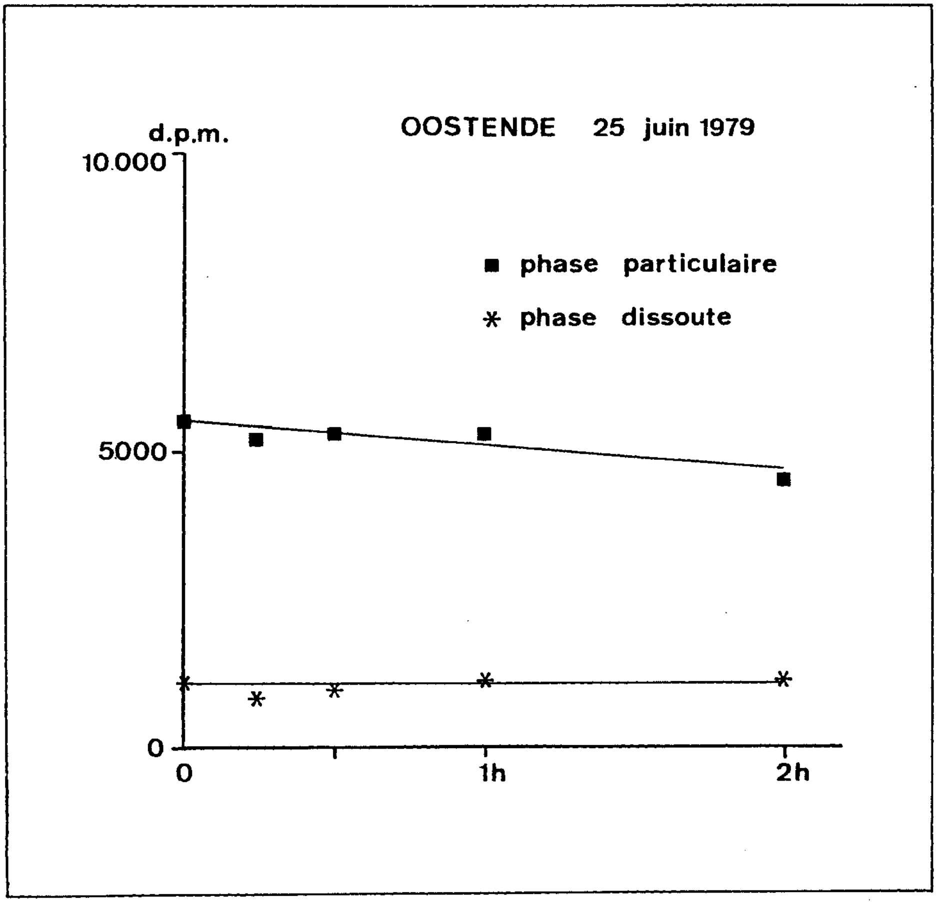

Fig.7 : Loosing of labelled CO_2 in the dark by phytoplankton.

molecular weight substances is not quickly used by micro-heterotrophs (see Lancelot et al, 1980).

Plate counts of bacteria present a distinct decrease from shore to sea in spring time (fig.8) ; at other periods, their distribution is homogeneous (Joiris, 1974). Glucose utilization rates show the same distribution (fig.9), higher rates characterizing the Belgian coastal zone compared with the more "Atlantic" water masses. The station "Ostend", for which more data on heterotrophic activities are available, seems reasonably representative of the whole area. Planktonic respiration rates, on the other hand, do not display any clear pattern of spatial distribution.

In order to determine the planktonic heterotrophic activity, the utilization of a given substrate was calculated as the product of its natural concentration in seawater and the relative utilization rate (reciprocal of the turnover time) obtained from the incorporation kinetic of the same radioactive substrate. The natural concentration of small substrates was shown to vary little around its equilibrium value set by the affinity of the microorganisms utilizing them (Billen et al, 1980). Most surveys of the concentration of amino acids or monosaccharides do indeed not reflect any significant seasonal evolution (e.g. Andrews & Williams, 1971 ; Crawford et al, 1974) : the variations of the absolute utilization rates are thus reflected by the variations of the relative rates. Available measurements of the relative utilization rates for glucose, amino acids and glycollate are plotted in fig. 10, these three compounds representing the three main classes of substrates directly utilizable by microheterotrophs : free mono- (and oligo) saccharides, free amino acids and organic acids resulting from phytoplankton excretion. The similarity between most values of determination of these three classes in various marine environments (table I) reflects again the efficiency of the control by microheterotrophs.

For calculating the heterotrophic activity in our area, following mean values of concentration were used : free monosaccharides : 0.8 $\mu mol.l^{-1}$ (60$\mu g\ C.l^{-1}$) ; free amino acids : 0.5 $\mu mol.l^{-1}$ (25 $\mu g\ C.l^{-1}$) ; glycollate : 2 $\mu mol.l^{-1}$ (50 $\mu g\ C.l^{-1}$). The obtained values are considered as provisional, since not all possible substrates were determined on the one hand, and on the other hand, since some substrates measured as "free" could, in some circumstances, not be available to the microheterotrophs (Gocke et al, 1981).

It is worth noticing that the total dissolved primary production (150g $C.m^{-2}.y^{-1}$) is able to account for the total heterotrophic activity of microorganisms (120g $C.m^{-2}.y^{-1}$). Even if less of 15% of this dissolved production is a low molecular weight one, the existence of an exoenzymatic hydrolyzing activity in water could explain the utilization of this production by bacteria (see chapter IV).

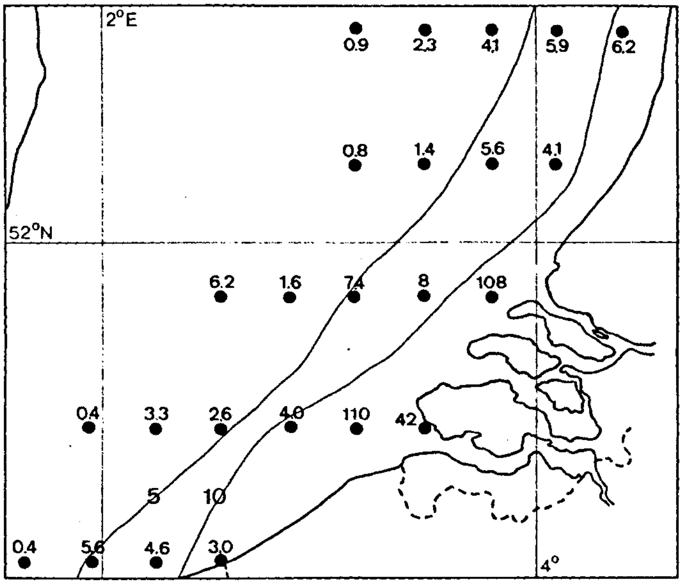

Fig.8 : Distribution of plate counts of bacteria in springtime.

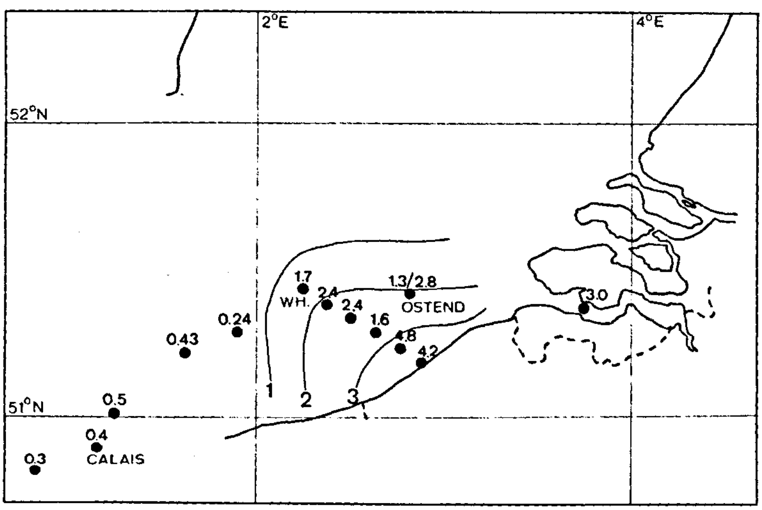

Fig.9 : Distribution of glucose utilization rates (% h^{-1})

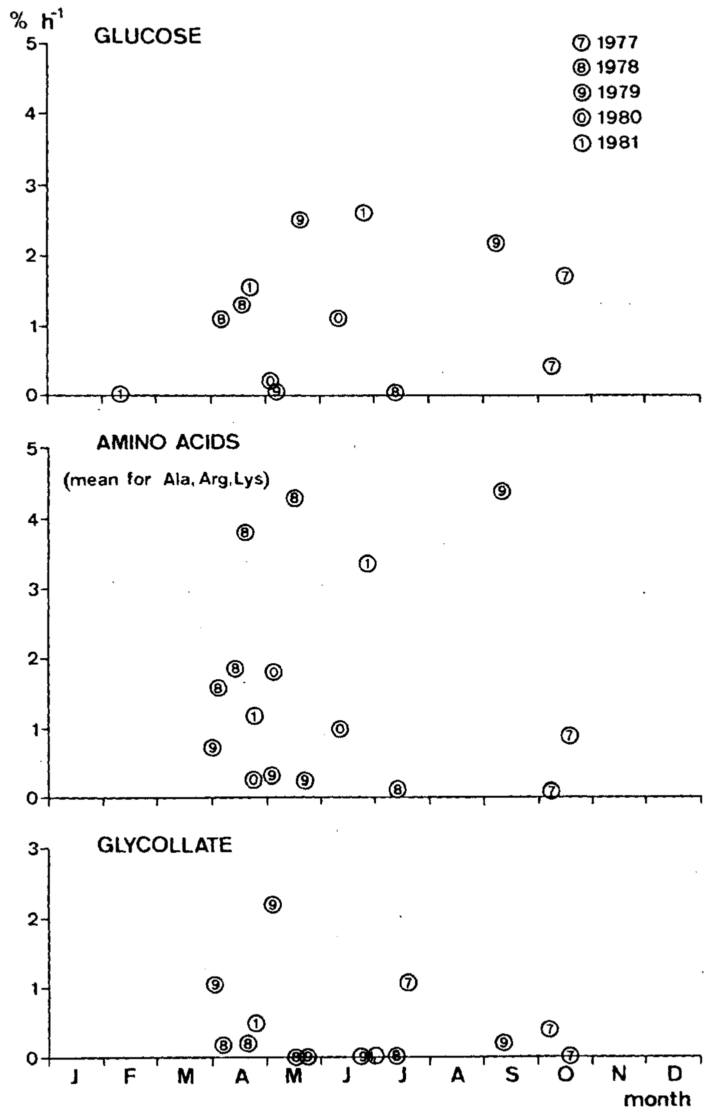

Fig.10 : Annual variation of relative utilization rates for glucose, amino acids and glycollate.

Table I

Determination of the main classes of substrates directly utilizable by microheterotrophs in various marine environments

Environment	Mean concentration (mole.1^{-1})	Authors
Free monosaccharides :		
North Atlantic	0.90	Burney et al, 1979
Gullmarfjord	0.86	Josefson, 1970
Narragansett Bay	0.88	Johnson & Sieburth, 1977
Sargasso Sea	0.58	Liebezeit et al, 1980
Free amino acods :		
North Atlantic	0.26	Pocklington, 1971
English Channel	0.26	Andrews & Williams, 1971
North Sea (Southern Bight)	0.51	Billen et al, 1980
Irish Sea	0.15	Riley & Segar, 1970
Baltic Sea	0.26	Dawson & Gocke, 1978
Glycollate :		
North Sea (Southern Bight)	2.25	Billen et al, 1980
Irish Sea	0.7	Al Hasan et al, 1975
Ipswich Bay	1	Shah & Wright, 1974
Ipswich Bay	0.5	Wright & Shah 1975
Essex River Estuary	0.26	Wright & Shah, 1975

d. Utilization of primary products by zooplankton

Zooplankton numbers and biomass, expressed as concentrations, are rather uniformely distributed, even if a slight increase from coast to open sea can sometimes be detected (fig.11). Owing to the greater depth of offshore stations, an increasing gradient appears when the biomass is expressed per area unit.

It has been observed that the various stages of zooplanktonic populations develop simultaneously in the whole studied area. At the station "West-Hinder" (51°23'00"N, 02°26'20"E), where most of the samples for zooplankton counts were obtained, zooplankton concentrations are very close to the mean value of the whole area.

Zooplankton counts obtained daily in 1978 at the station "West-Hinder" show three main peaks from April to July, mainly formed by copepods (fig.12). From one year to another, however, the peaks can be quantitatively different (Bossicart, 1980).

Zooplankton organic content was determined at 20 stations, on samples taken monthly (table II)(Hecq et al, 1980). The mean annual value of zooplankton biomass is 0.2g $C.m^{-2}$. The date on respiration activity of zooplankton, determined by oxygen consumption rate (table III) show a peak in zooplankton respiration during the period April-May and also important variations of respiration rate (per unit of biomass), with high rates corresponding with the growing phase of zooplankton (Hecq, unpublished results). The mean value of zooplanktonic respiration is 26g $C.m^{-2}.y^{-1}$. Data on grazing activity of herbivorous zooplankton on living phytoplankton (fig.13) show a peak in mid-May. An October peak was found in experiments carried out during a short period in 1977 ; these results still have to be confirmed.

It appears therefore that the first peak of zooplankton is related to the phytoplankton bloom in the spring but that the two other ones are not related to phytoplankton biomass. It is moreover worth noticing that only 40% of the net particulate primary production (80g $C.m^{-2}.y^{-1}$; 20% of the total net) is grazed by zooplankton. This can be explained by the fact that grazing reveals to occur only on the 25-100 μ size classes of phytoplankton which are the less abundant during the period of grazing activity (see chapter IV).

e. The detritus - benthic organisms relations

Most of the particulate primary production remaining ungrazed is converted in detritus which settles down to the sediments (fig.2).

The composition and distribution of sediments in the Eastern Southern Bight of the North Sea have been described in detail by Gullentops (1974) and Wollast (1976). The greater part of the bottom consists of rather coarse sandy deposits, with much gravels and shell fragments, particularly in the Southwestern part. The Belgian coastal zone, on the other hand, is characterized by finer sediments, with a higher content in organic matter. Organic mat-

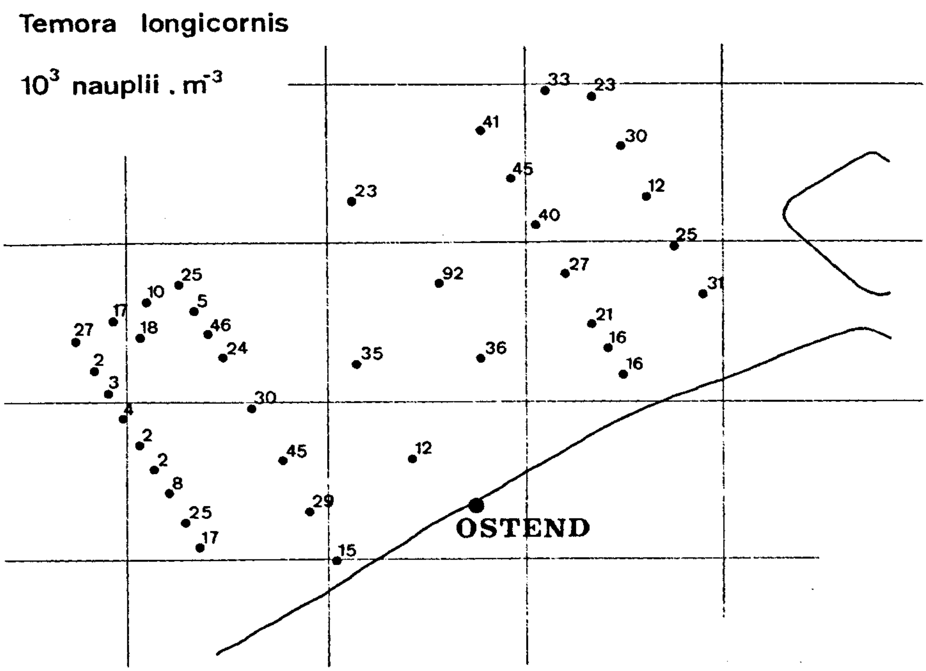

Fig.11 : Distribution of *Temora longicornis*.

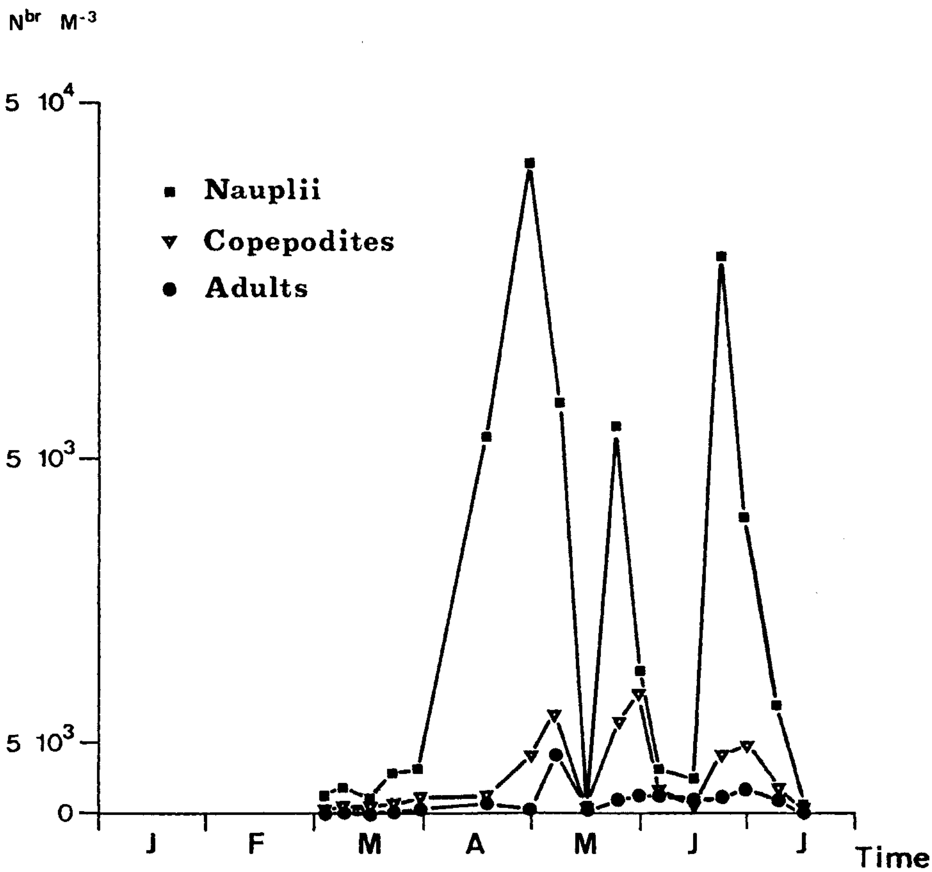

Fig.12 : Annual variation of Copepods' biomass.

Table II

Mean zooplankton organic content (proteins + carbohydrates + lipids- in monthly samples taken in 1979 and 1980 at 20 stations of the Belgian coastal zone

Month		n(1)	Zooplankton organic matter $mg.m^{-3}$ ± S.D.
1979	February	1	0(2)
	May	1	250
	June	16	490 ± 80
	July	18	60 ± 15
	September	12	10 ± 5
	October	16	0
	November	13	15 ± 5
1980	January	20	0
	February	16	0
	March	13	0
	May	19	0
	June	11	40 ± 7
	July	11	0
	September	16	45 ± 6
	October	19	30 ± 5
	November	20	30 ± 7

(1) n : number of samples

(2) o : not detectable : < 10

Table III

Mean values of zooplankton respiration rate in the Belgian coastal zone for the period 1973-1975

Month	(n)	Respiration rate per biomass unit mg C. mg $C^{-1}.d^{-1}$ ± S.D.	Zooplankton respiration mg $C.m^{-3}.d^{-1}$
January 1973	3	0.07 ± 0.04	0.28
February 1975	7	0.03 ± 0.01	0.03
April 1973(1)	3	0.43 ± 0.07	5.59
April 1973(2)	8	0.60 ± 0.10	4.02
April 1974(1)	3	0.68 ± 0.16	17.10
April 1974(2)	6	0.30 ± 0.18	1.17
April + May 1975	11	0.24 ± 0.07	12.0
May 1973(3)	12	0.84 ± 0.06	4.79
May 1974(4)	7	0.12 ± 0.04	6.72
May 1974(5)	4	0.06 ± 0.03	1.86
June 1975	9	0.26 ± 0.04	5,20
July 1975	9	0.17 ± 0.04	2.89
September 1975	3	0.58 ± 0.13	9.28
Sept. + Oct. 1974	7	0.18 ± 0.05	3.42
October 1975	9	0.10 ± 0.01	1.08
Nov. + Dec. 1974	3	0.10	0.2
Integrated annual mean		0.21	4.0

(1) Second decade ; (2) third decade ; (3) first week ; (4) second week ;
(5) last week.

ter content of the upper 1 cm of the sediment was used as an index of the importance of the flux of depositing organic carbon (see e.g. Billen, 1982). Thus, the geographic distribution of ignition loss of the bottom sediments (fig.14) indicates a higher flux of sediment organic matter in the coastal zone than in the offshore zones. This is particularly true in a region of mud accumulation just in front of the Belgian coast.

The quantitative importance of the benthos in recycling organic matter in the Belgian coastal zone shows that an important part of primary production settles down on the sediments. Faecal pellets and zooplankton corpses can only make up a small fraction of this flux : it is therefore likely that phytoplankton cells and - detritus constitute the bulk of the organic matter flux to the sediments.

A direct confirmation was obtained in the area of mud accumulation off the coast, where vertical distribution of chlorophyll and of particulate nitrogen in the sediment was determined (fig. 15), showing the importance of benthos in the recycling of the organic phytoplanktonic matter.

f. Conclusions

Accumulation of data on the carbon budget in the Belgian coastal zone clearly shows that zooplankton grazing is not the main cause of phytoplankton mortality, as it was generally expected for marine ecosystems : planktonic and benthic microheterotrophs play the predominant role in recycling primary production. From literature data, this could be the situation in all coastal seas, as opposed to open sea systems.

This is confirmed by the comparison of data from "Ostend" and "Westhinder" compared to open sea and estuarian ecosystems as shown in the part 2 of this chapter.

From the results presented in the previous section, the integrated mean fluxes of carbon between the main compartments were calculated, in order to build up a budget of carbon cycling within the ecosystem. This was done for a complete year, on the one hand, and on the other hand for the vernal period (15 March - 15 July), including the main peaks of activity : spring phytoplankton and main zooplankton blooms. These results are summarized in table IV ; the annual budget is diagramatically summarized in fig.2.

As seen in this figure, the annual budget is fairly balanced, as far as the fate of net primary production is concerned. It must first be noted that exogenous - i.e. terrestrial - imports of organic matter are negligible with respect to endogenous production : domestic and industrial discharges from the Belgian coast represent a maximum of 4000 tons C per year, and the import by the Scheldt estuary has been estimated as 9000 tons C per year (Wollast, 1976). This amounts to about 2.5g $C.m^{-2}\ a^{-1}$ for the whole coastal zone, representing less than 1% of the primary production.

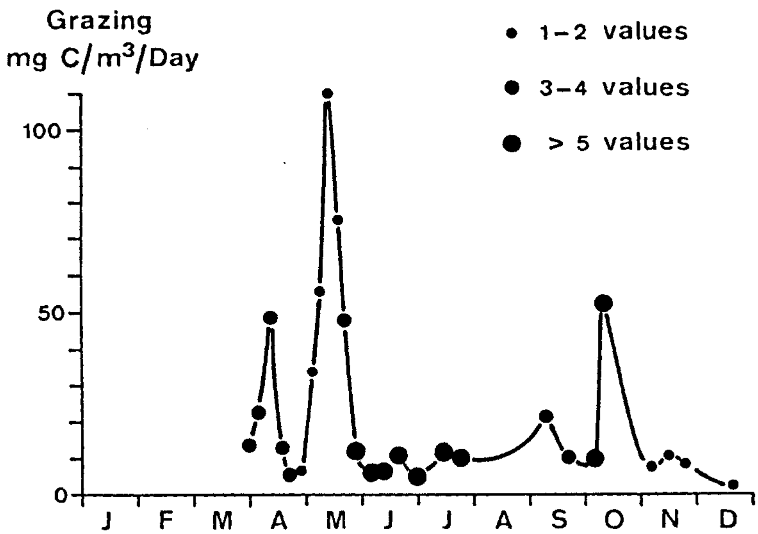

Fig.13 : Annual variation of grazing activity of zooplankton.

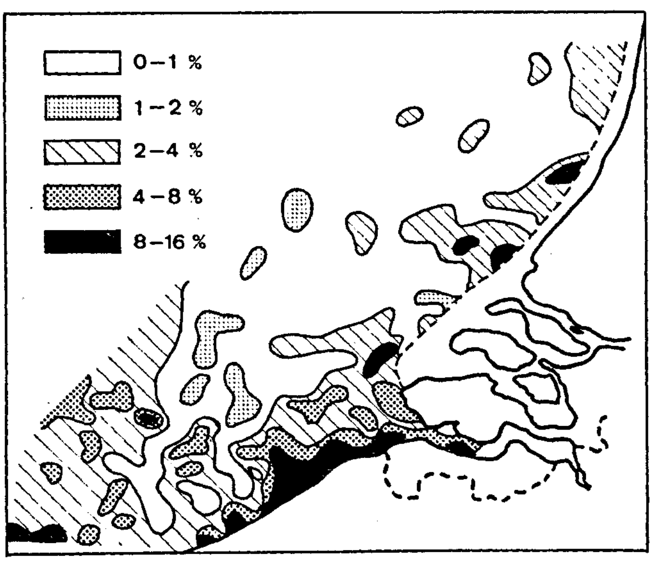

Fig.14 : Geographic distribution of ignition loss of the bottom sediments (after Wollast, 1976).

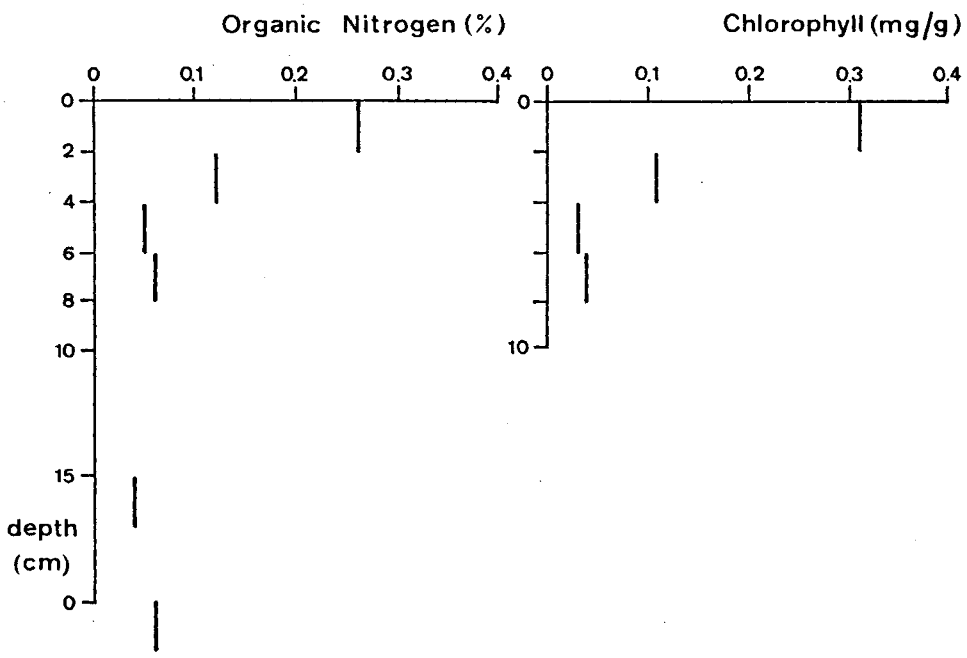

Fig.15 : Vertical distribution of chlorophyll and particulate nitrogen in the sediment.

Table IV

Annual and vernal budget of carbon cycling in the Belgian coastal zone

	Annual budget	Vernal budget (15 March-15 July)
Mean biomass	g $C.m^{-2}$	g $C.m^{-2}$
Phytoplankton	3.7	5.5
Detritus	4.3	4.9
Zooplankton	0.3	0.4
Mean fluxes		
Primary production :		
- net particulate	170	110
- dissolved	150	105
- total net	320	215
Zooplankton grazing	80	40
Zooplankton respiration	22	11
Microheterotrophic activity	120	70
Benthic mineralization	155	55
Benthic fossilization	5	-
Planktonic oxygen consumption	2000	1000

Of the total net primary production, only 20% (40% of the net particulate production) is grazed by zooplankton, while 40% (80% of the dissolved production) is consumed by planktonic microheterotrophs, the rest (about 40%) being degraded by the benthic microorganisms.

A major unbalance appears, however, when the estimation of the total planktonic oxygen consumption is converted into carbon flux and compared with the figures of primary production, the former being much higher than the latter : this unbalance was already detected a few years ago (Joiris, 1977).

This total planktonic oxygen consumption comprises respiration by microheterotrophs, by phytoplankton and by zooplankton.

If our estimates of microheterotrophic activity and of zooplankton respiration are accepted, they clearly cannot explain the high values of total respiration. On the other hand, some preliminary determinations of phytoplanktonic respiration, measured after incubation at maximal light intensity, show decrease of incorporated radioactivity at a rate of about 10% of phytoplankton biomass per hour. Extrapollating this rate to the whole water column and to the 24 hours-day considering that day and night phytoplanktonic respirations are identical, one can calculate a value of phytoplankton respiration of about 3000g $C.m^{-2}.a^{-1}$, in reasonable agreement with the measured planktonic oxygen consumption rate : this implies that the phytoplankton respiration could be, by far, the main element of the total plankton respiration.

This unexpected interpretation is in contradiction with most published budgets of aquatic ecosystems. But, in the frame of the contradiction between gross primary production and much higher consumption rates in various marine systems (Sorokin, 1973 ; Sieburth, 1976 ; Joiris, 1977), it offers however an explanation : in most cases, phytoplankton respiration was calculated as a percentage of primary production (Steemann Nielsen, 1952), which leads to much lower estimations than in our proposition, and could roughly underestimate the gross primary production, especially in deeper water masses.

2° Comparizon of carbon cycling in the belgian coastal zone with other marine systems.

Although classical textbooks have presented marine systems in general as grazing ecosystems, as opposed to terrestrial ecosystems where detritus food chains dominate (Cushing, 1958 ; Crisp, 1964 ; Odum, 1972 ; Steele, 1974), this conception seems to hold only for oligotrophic open ocean systems. Table V summarizes the results of recently published studies, from which it has been possible to calculate the part of net primary production consumed by zooplankton and bacterioplankton respectively. In table VI, the same kind of comparizon is made with data recolted in the Central North Sea (Fladenground, FLEX 76) with the same kind of techniques as in the Belgian coastal zone. Table VII compares some carbon fluxes in stations "Calais-Boulogne", "Ostend", "Westhinder"

Table V

Survey of the literature on the relative role of zooplankton and bacterioplankton in recycling primary production

Environment	Authors (§)	Zooplankton grazing % particulate primary production	Bacterioplankton activity % particulate primary	Bacterioplankton activity % dissolved production
<u>Coastal systems</u>				
Belgian coastal zone	1	40	-	80
Cochin estuary (India)	2	15	-	-
Long Island sound	3	26	-	-
Soanish Inlet (Canada)	4	-	68	-
English Channel	5	-	100	-
Akkeshi Bay	6	10	-	-
Gulf of Mexico	7	3	-	-
Texas coastal zone	7	33	-	-
Behring sea	7	10	-	-
La Jolla (California)	4	-	56	-
Baltic Sea	8	-	-	91
Southern California Bight	9	7.5	101	-
Saonish Inlet (Canada)	9	11	91	-
Black Sea	10	5 - 25	-	-
Washington coastal zone	11	3	-	-
<u>Upwelling area</u>				
Peru	12	6	78	-
<u>Open sea systems</u>				
Fladenground (North Sea)	13	100	-	-
Tropical Pacific	14	75	-	-
	15	90	-	-
Sargasso Sea	16	100	-	-
Pacific off Oregon	11	36	-	-
Sub tropical Pacific	17	40	-	-
		110	-	-

(§) 1) this work ; 2) Oasin, 1970 ; 3) Riley, 1956 ; 4) Furhman & Azam, 1979; 5) Andrews & Williams, 1971 ; 6) Hogetsu, 1979 ; 7) Walsh et al, 1981 ; 8) Larsson & Azam, 1979 ; 9) Harrison, 1978 ; 10) Grefe, 1970 ; 11) Jawed, 1973 ; 12) Walsh, 1981 & Sorokin, 1978 ; 13) Daro, 1980 ; 14) Steemann Nielsen, 1972 ; 15) Shuskina & Vinogradov, 1979 ; 16) Menzel & Ryther, 1961 ; 17) Eppley et al, 1973.

Table VI

Comparison between two biotopes of the North Sea : the Belgian coastal zone and the Fladenground (Flex 76). (Both data sets concern the period May-June).

	Southern Bight (a)	Fladenground (b)	
Phytoplankton biomass ($g\ C.m^{-2}$)	10	5 - 10	(1)
Particulate primary production ($g\ C.m^{-2}\ d^{-1}$)	1	0.5 - 1.5	(2)
Zooplankton biomass ($g\ C.m^{-2}$)	0.3	3.6	(3)
Grazing ($g\ C.m^{-2}\ d^{-1}$)	0.3	1 - 2	(4)

(a) Present study

(b) Results from : 1) Brockmann et al, unpubl. results
2) Weigel & Hagmeier, unpubl. results
3) Krause & Radach, 1980
4) Daro, 1980

Table VII

Comparison between some carbon fluxes in stations "Calais-Boulogne", "Ostend-Westhinder" and "Hansweert"

	Calais-Boulogne	Ostend-Westhinder	Hansweert
BOD_5	0.6g $C.m^{-3}$	1.0g $C.m^{-3}$	1.3g $C.m^{-3}$
Heterotrophic activity	6g $C.m^{-3}.y^{-1}$	8g $C.m^{-3}.y^{-1}$	38g $C.m^{-3}.y^{-1}$
Total planktonic respiration	61g $C.m^{-3}.y^{-1}$	133g $C.m^{-3}.y^{-1}$	78g $C.m^{-3}.y^{-1}$
Particulate net production :			
April 1981	25 mg $C.m^{-3}d^{-1}$	67mg $C.m^{-3}d^{-1}$	
September 1981	7 mg $C.m^{-3}d^{-1}$	17mg $C.m^{-3}d^{-1}$	
Grazing : May 1979 (-3m)	7.0mg $C.m^{-3}d^{-1}$	40 mg $C.m^{-3}d^{-1}$	
September 1979 (-3m)	0.4mg $C.m^{-3}d^{-1}$	10 mg $C.m^{-3}d^{-1}$	

and "Hansweert". All these data quite clearly show that in coastal and upwelling systems zooplankton grazing usually represents less than 40-30% of the net particulate primary production, while it consumes more than 40%, and often up to 100% of it in open sea systems.

On the other hand, the part of primary production being degraded in the benthos is known to be inversely related to the depth of the water column (Suess & Müller, 1980).

These different remarks lead to the following general picture : the food chain initiated by zooplankton grazing and leading to pelagic fish is more efficient when primary production is diluted in a deep euphotic zone, i.e. when predators actively hunting their food have an advantage. On the contrary, when important primary production is concentrated in shallow ecosystems, most of it is recycled by microheterotrophs, in the water and in the sediments.

REFERENCES

ANDREWS, P. & WILLIAMS, P.J., (1971). Heterotrophic utilization of dissolved organic compounds in the sea. *J. Mar. Biol. Ass. U.K.*, 51, 111-125.

AL HASAN, R.H., COUGLAN, S.J., PANT, A. & FOGG, G.E., (1975). Seasonal variations in phytoplankton and glycollate concentration in the Menai Strait. *J. Mar. Biol. Ass. U.K.*, 55, 557-565.

BILLEN, G., (1982). *Modelling the processes of organic matter degradation and nutrient recycling in sedimentary systems* in *Sediment Microbiology*, D.N. Nedwell (Ed.), Academic Press, 15-52.

BILLEN, G., JOIRIS, C., WIJNANT, J. & GILLAIN, G., (1980). Concentrations and metabolisation of small organic molecules in estuarine, coastal and open sea environments in the Southern North Sea. *Est. Coast. Mar. Sci.*, 11, 279-294.

BOSSICART, M., (1980). Population dynamics of copepods in the Southern Bight of the North Sea (1977). *I.C.E.S.*, C.M. 1980/L:24.

BURNEY, C.M., JOHNSON, K.M., LAVOIE, D.M. & SIEBURTH, Mc N., (1979). Dissolved carbohydrates and microbial ATP in the North Atlantic : concentrations and interactions. *Deep Sea Res.*, 26A, 1267-1290.

CRAWFORD, C.C., HOBBIE, J.E. & WEBB, K.L., (1974). The utilization of dissolved free amino acids by estuarine micro-organisms. *Ecology*, 55, 551-563.

CRISP, D. (Ed.), (1964). *Grazing in terrestrial and marine environments*. Blackwell Sci. Publ. Oxford, 322 pp.

CUSHING, (1958). The effect of grazing in reducing the primary production : a review. *Rapp. P.V. Réun. Cons. Perm. Int. Explor. Mer*, 144, 149-155.

DARO, M.H., (1980). Field study of the deel feeding of a population of *Calanus finmarchicus* at the end of a phytoplankton bloom. *Meteor. Forsch. Ergb. R.A.*, 22, 123-132.

DAWSON, R. & GOCKE, K., (1978). Heterotrophic activity in comparison to the free amino acid concentrations in Baltic sea water samples. *Oceanol. Acta*, 1, 45-54.

EPPLEY, R.W., RENGER, E.H., VENRICK, E.L. & MULLIN, M.N., (1973). A study of plankton dynamics and nutrient cycling in the central gyre of the North Pacific Ocean. *Limnol. Oceanogr.*, 18, 534-551.

FUHRMAN, J.A. & AZAM, F., (1979). Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. *Appl. Environ. Microbiol.*, 1085-1095.

GOCKE, K., DAWSON, R. & LIEBEZEIT, G., (1981). Availability of dissolved free glucose to heterotrophic microorganisms. *Mar. Biol.*, 62, 209-216.

GULLENTOPS, F., (1974). *Detrital sedimentology in the Southern Bight of the North Sea*, in *Math. Modelsea, I.C.E.S., Hydrography Committee*, CM 1974 : C-1 : 55-80.

GREFE, V.N., (1970). *The biomass and production of different trophic levels in the pelagic communities of South Seas in Marine Food chairs*. J.H. Steele, Oliven & Boyd, Edinburgh.

HARRISSON, W.G., (1978). Experimental measurements of nitrogen remineralization in coastal waters. *Limnol. Oceanogr.*, 23, 684-694.

HECQ, J.H., GASPAR, A. & PICARD, H., (1980). Spatial pattern and biochemical content of North Sea zooplankton (Belgian coast)(1979-1980). *I.C.E.S.*, 1980.

HOGETSU, K., (1979). *Biological productivity of some coastal region of Japan in marine production mechanisms*. IBP (Ed.), Dunbar. Cambridge University Press.

JAWED, N., (1973). Ammonia excretion by zooplankton and its significance to primary productivity during summer. *Mar. Biol.*, 23, 115-120.

JOHNSON, K.M. & SIEBURTH, J.Mc N., (1977). Dissolved carbohydrates in seawater. I. A precise spectrophotometric analysis for monosaccharides. *Mar. Chem.*, 5, 1-13.

JOIRIS, C., (1974). Variations spatiales et temporelles de la concentration bactérienne dans les eaux du Sud-Est de la Mer du Nord. *Ann. Soc. Roy. Zool. Belg.*, 104, 39-50.

JOIRIS, C., (1977). On the role of heterotrophic bacteria in marine ecosystems: some problems. *Helgoländer Wiss. Meeresunters*, 30, 611-621.

JOSEFFSON, B.R., (1970). Determination of soluble carbohydrates in sea water by partition chromatography after desalting by ion-exchange membrane electro-dialysis. *Anal. Chim. Acta*, 52, 65-73.

KRAUSE, M. & RADACH, G., (1980). On the succession of developmental stages of herbivorous zooplankton in the northerh North Sea during FLEX '76. 1. First statements about the main groups of the zooplankton community. *"Meteor" Forsch. Ergebnisse*, 22, 133-149.

LANCELOT, C., (1980). A statistical method to estimate the biochemical composition of phytoplankton in the Southern Bight of the North Sea. *Est. Coast. Mar. Sc.*, 10, 467-478.

LANCELOT, C., DARO, M.H., BOUQUEGNEAU, J.M., BILLEN, G., JOIRIS, C., BOSSICART, M., BERTELS, A., VERBEUSTEL, S., NYS, J., NIHOUL, C., PUTMAN, J., WIJNANT, J., HEISE, A. & GOEYENS, L., (1979). Ecometabolism of the coastal area of the Southern Bight of the North Sea. Report of the workgroup "Organic Matter". *I.C.E.S.* C.M. 1980/L:22. Biological Oceanography Committee.

LARSSON, U. & HAGSTROM, A., (1979). Phytoplankton exudate release as energy source for the growth of pelagic bacteria. *Mar. Biol.*, 52, 199-206.

LIEBEZEIT, G., BOLTER, M., BROWN, I.F. & DAWSON, R., (1980). Dissolved free amino acids and carbohydrates at pycnocline boundaries in the Sargasso Sea and related microbial activity. *Oceanol. Acta*, 3, 357-362.

MENZEL, D.W. & RYTHER, J.H., (1961). Zooplankton in the Sargasso Sea of Bermuda and its relation to organic production.

MOENS, M., (1974). Suspended matter. *Math. Modelsea, I.C.E.S.*, Hydrography Committee, CM 1974 C/1 , 81-91.

MOMMAERTS, J.P., (1973a). The relative importance of nannoplankton in the North Sea primary production. *Br. Phycol. J.*, 8, 13-20.

MOMMAERTS, J.P., (1973b). On primary production in the South Bight of the North Sea. *Br. Phycol. J.*, 8, 217-231.

NIHOUL, J.C.J. & RONDAY, F.C., (1975). The influence of the tidal stress on the residual circulation. *Tellus*, 27, 484-489.

OASIN, S.F., (1970). *Some problems related to the food chain in a tropical estuary*, in *Marine Food Chains*. J.H. Steele (Ed.), Oliver & Boyd, Edinburgh.

ODUM, E.P., (1971). *Fundamentals of Ecology*. Saunders, Philadelphia, London, Toronto, 574 pp.

POCKLINGTON, R., (1971). Free amino acids dissolved in North Atlantic Ocean waters. *Nature*, 230, 374-375.

RILEY, G.A., (1956). Oceanography of Long Island Sound. 1952-1954. IX. Production and utilization of organic matter. *Bull. Bingham Oceanogr. Collect. Yale Univ.*, 15, 324-344.

RILEY, J.P. & SEGAR, D.A., (1970). The seasonal variation of the free and combined dissolved amino acids at a station in the Irish Sea. *J. mar. biol. Ass. U.K.*, 50, 713-720.

SUGIURA, Y., IBERT, E.R. & HOOD, D.W., (1963). *J. mar. Res.*, 21 , 11.

SHAH, N.M. & WRIGHT, R.T., (1974). The occurence of glycollic acid in coastal seawater. *Mar. Biol.*, 24, 121-124.

SHUSKINA, E.A. & VINOGRADOV, N.E., (1979). *Trophic relationship in communities and the functioning of marine ecosystems. II. Some results of investigations on the pelagic ecosystems in tropical regions of the Ocean, Marine production mechanisms*. IBP (Ed.), Dunbar. Cambridge University Press.

SIEBURTH, J.Mc N., (1976). Bacterial substrates and productivity in marine ecosystems. *Ann. Rev. Ecol. Syst.*, 7, 259-285.

SOROKIN, Y.I., (1973). Data on biological productivity of the western tropical Pacific Ocean. *Mar. Biol.*, 20, 177-196.

SOROKIN, Y.I., (1978). Description of primary production and of the heterotrophic microplankton in the Peruvian upwelling region. *Oceanology*, 18,(1), 62-71.

STEELE, J.H., (1974). *The structure of marine ecosystems.* Harvard University Press, Cambridge, Massachusetts, 128 pp.

STEEMANN NIELSEN, E., (1952). The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *J. Cons. Perm. int. Explor. Mer.*, 18, 117-140.

STEEMANN NIELSEN, E., (1972). The rate of primary production and the size of standing stock of zooplankton in the Ocean. *Int. Rev. Ges. Hydrobiol.*, 57, (4), 513-516.

SUESS, E. & MULLER, P., (1980). *Productivity, sedimentation rate and sedimentary organic matter in the Oceans. II. Elemental fractionation*, in *Colloques internationaux du C.N.R.S.*, n° 293. Biogéochimie de la matière organique à l'interface eau-sédiment marin.

WALSH, J.J., (1981). A carbon budget for overfishing off Peru. *Nature*, 290, 300-304.

WALSH, J.J., ROWE, G.T., IVERSON, R.L. & ROY, P.Mc, (1981). Biological export of shelf carbon in a sink of the global CO_2 cycle. *Nature*, 291, 196-201.

WOLLAST, R., (1976). *Transport et accumulation de polluants dans l'estuaire de l'Escaut*, in *L'Estuaire de l'Escaut.* Programme national de recherche et de développement. Environnement Eau. Projet Mer, vol. 10, J.C.J. Nihoul & R. Wollast (Eds), Bruxelles.

WRIGHT, R.T. & SHAH, N.M., (1975). The trophic role of glycollic acid in coastal seawater. I. Heterotrophic metabolism in seawater and bacterial cultures. *Mar. Biol.*, 33, 175-183.