

OXYGEN REGIME, RESPIRATORY ACTIVITY AND BIOMASS OF MICROORGANISMS, AND THE CARBON BUDGET IN THE FLADEN GROUND AREA (NORTHERN NORTH SEA) DURING SPRING

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ABSTRACT

A watermass, on the Fladen Grounds, marked with a drifting buoy, was studied daily during one month in spring. Hydrographic parameters, nutrient regime, oxygen regime, biomass of microorganisms and respiratory activity were determined; the high variability of the observations is discussed. From these observations, and earlier publications on the same cruise, a carbon budget is calculated. From oxygen flux calculations it appeared that the net ecosystem production must be more than $2.5 \text{ g C m}^{-2} \cdot \text{d}^{-1}$ which could not be verified by C-14 primary production measurements. Presumably high variability in the system in time and space makes it impossible to get a fitting budget.

1. INTRODUCTION

During spring 1983, a multidisciplinary foodweb study has been made in the Northern North Sea, in the Fladen Ground Area. This Reflex (Repeated Fladenground Expedition) was a follow up of the Fladen Ground Experiments Preflex (1975) and Flex (1976). These expeditions intended to contribute to a quantitative understanding of the dynamics of phytoplankton, zooplankton and benthos in this area (LENZ *et al.* 1980; RADACH 1980; RADACH *et al.* 1984; DAVIES & PAYNE, 1984).

In the Reflex study changes in the ecosystem of a moving watermass in time, from 28 April to 25 May 1983 were followed. To this end the water mass was marked with a large drogue in the 8-15 m depth layer. Fig. 1 gives the research area and the traject the drifter followed during the research period. Mean depth of the water column was 125 m.

From published results from this cruise we know that the surface waters were supersaturated with oxygen at the beginning of the cruise and oxygen percentages further increased to almost 140% at the end of May, causing a large oxygen flux to the atmosphere (TIJSSEN, 1986). A succession of phytoplankton species was

observed during this spring bloom by CADÉE (1985). He observed at the beginning of the cruise *Chaetoceros* spp., including large chain formers and they were followed by peaks in abundance of *Emiliana huxleyi* and a small centric diatom *Thalassiosira conferta*. After 14 May a colonial flagellate (*Corymbellus aureus*) and other unidentified microflagellates were dominant.

In this system, with the wax and wane of different plankton species, we have studied the nutrient regime, the respiratory activity and biomass in the water column. In two undisturbed sediment cores the distribution of biomass in the upper 13 cm has been measured. The variability of observations in a time series and in space will be shown. Oxygen and carbon budgets will be completed with results of studies on POC, DOC, sedimentation (CADÉE, 1986), primary production (GIESKES & KRAAY, 1986), activity of bottom fauna (DE WILDE *et al.*, 1986) and secondary production (FRANZ & DIEL, 1986). All these studies were done at the same cruise in the same water mass.

Acknowledgments.—M. Mulder took responsibility for a large part of the onboard hydrographic work and oxygen determinations. The cruise was financially supported by the Netherlands Council for Oceanic Research. The comments of two referees and editor on an earlier draft of this paper are acknowledged.

2. METHODS

The water mass was marked with a window shade drogue of 30 m^2 (MULDER & MANUELS, 1982), which could be traced by radiosignals transmitted from a small, surface radio buoy and a direction-sensitive receiver.

Watersampling was performed with a rosette sampler equipped with eleven 30 l Niskin bottles. A Guildline 8705 CTD sensor package interfaced with a HP 9825A processor provided depth, temperature and salinity readings down- and upcast. Calibration temperatures were obtained from reversing thermometer readings. Control salinities were determined on an Autosol 8400 A salinometer.

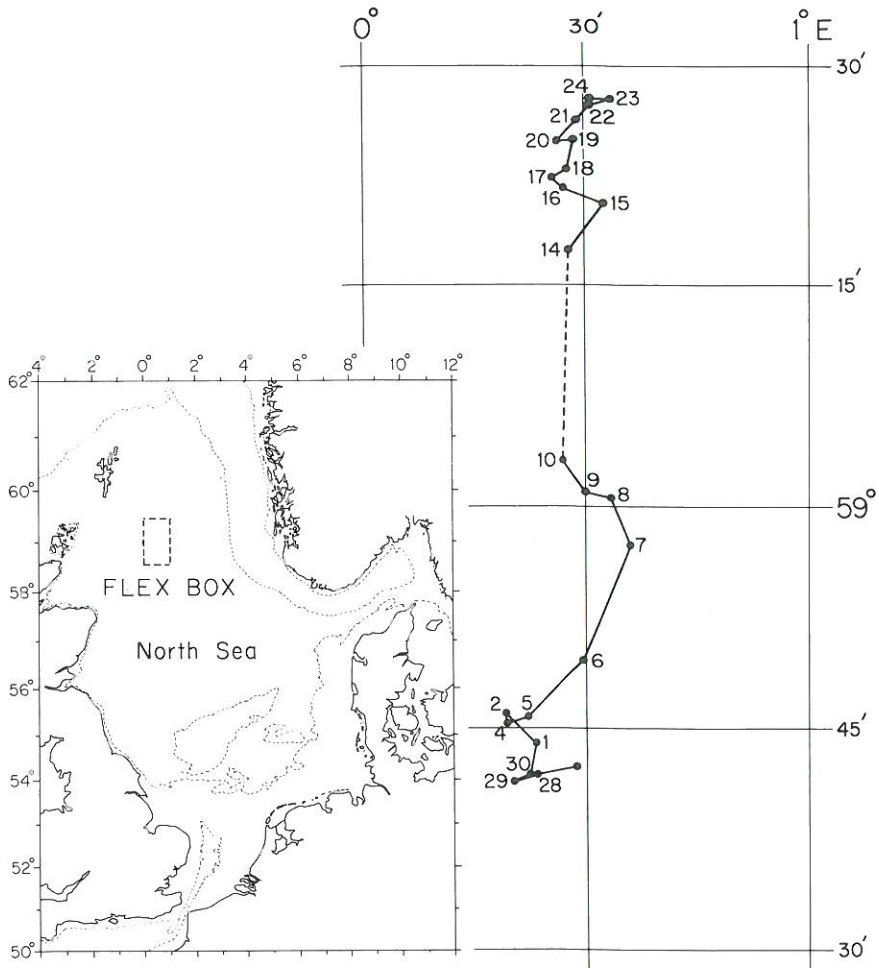


Fig. 1. The Flex box area and the traject the drifter followed during the cruise from 28 April to 24 May 1983.

Filtered water samples were deepfrozen onboard and analyzed afterwards for nutrients at the institute, using automated STRICKLAND & PARSONS (1972) methods.

Dissolved oxygen was determined on board in triplicate, usually within 24 hours after addition of reagents, applying a high precision photometric Winkler determination (TIJSSSEN, 1981) in a half-automated, computerized version (TIJSSSEN *et al.*, 1989). Triplicate analysis precision is better than 0.1% ($P=0.9$). Accuracy is (estimated to be) better than 0.2%.

Biomass of microorganisms (bacteria, small phytoplankton and zooplankton) was analysed by measuring the ATP content in watersamples prefiltered over a 50 μm gauze. Multiplying the ATP content with a factor 250 gives the biomass in carbon (C) units. In marine ecology this factor is usually accepted (KARL, 1980). For ATP as a biomass estimation we used the method described by VOSJAN (1988) and VOSJAN *et al.* (1987) which is a modification of the originally described

method of HOLM-HANSEN & BOOTH (1966).

The respiratory electron transport system (ETS) activity as a relative measurement for respiration rate is originally described by PACKARD (1971). Prefiltered water samples (50 μm gauze) were filtered over a 0.2 μm nuclepore filter and the collected microorganism incubated in a substrate-buffer solution (OLANCZUK-NEYMAN & VOSJAN, 1977). The method gives a potential respiration rate. The method is quick and easy, so in research with dense station nets as in mapping oceanography it is very useful (VOSJAN & NIEUWLAND 1987; VOSJAN 1988).

3. RESULTS AND DISCUSSION

3.1. HYDROGRAPHY AND NUTRIENT REGIME

Residual current direction for the whole period was true north with a mean velocity of $0.037 \text{ m}\cdot\text{s}^{-1}$. The net

wind direction was SE. From 28 April to 5 May northerly winds, 8 m.s^{-1} , prevailed and the associated drift was slowly northward. From 6 May to 15 May southeasterly winds, 10.5 m.s^{-1} were common, which caused strong drift to the north and from 16 May to 24 May weak westerlies of 5.3 m.s^{-1} were accompanied with an irregular slow northward drift. Mean wind speed over the whole period was 8.0 m/s . (see Fig. 1.)

Vertical temperature differences were at first small (0.2° C .) and at the end of May the formation of the seasonal thermocline was still at its infancy (TIJSSSEN, 1986). The steep temperature rise in the last week was only observed in the upper 10 m during a period of low wind strength. At the surface the temperature increased from 6.8 on 28 April to 9.0° C . on 24th May (Fig. 2 a).

Salinities did not vary much, at the surface from 35.15 to 35.2 and at 120 m depth from 35.05 to 35.15 (Fig. 2 b).

A west-east section in the Northern North Sea crossing the southern part of the Flex box end March 1976 (SVANSON, 1980) showed rather homogeneous conditions vertically and horizontally in the FLEX box obviously characteristic for pre-spring-bloom conditions. (Table 1). WEICHAART (1980) observed the spring bloom

TABLE 1

Hydrographic characteristics in the Flex box end of March 1976. (SVANSSON, 1980).

salinity	35.1-35.15
temperature	6.1- 6.3 $^\circ\text{C}$
total sol P	0.7 $\text{mmol}\cdot\text{m}^{-3}$
total part P	<0.05 $\text{mmol}\cdot\text{m}^{-3}$
NO_3	8-9 $\text{mmol}\cdot\text{m}^{-3}$
POC	10 $\text{mg C}\cdot\text{m}^{-3}$

in 1976 at the central station in the Flex box. His nutrient observations clearly show the transition from nearly homogeneous nutrient concentrations in the vertical to much lower concentrations in the upper 50 m. In 12-14 days a decline was seen from 8 to $4 \text{ mmol}\cdot\text{m}^{-3} \text{ NO}_3$ and from 0.55 to $0.4 \text{ mmol}\cdot\text{m}^{-3} \text{ PO}_4$; another four days later nitrate fell to $< 1 \text{ mmol}\cdot\text{m}^{-3}$ and phosphate to $< 0.25 \text{ mmol}\cdot\text{m}^{-3}$. EBERLEIN *et al.* (1980) observed an NH_4 increase of $0.5\text{-}1.5 \text{ mmol}\cdot\text{m}^{-3}$ at the central station from 23 April to 13 May in a major part of the water column.

During Reflex we measured nutrient concentrations of $4 \text{ mmol}\cdot\text{m}^{-3} \text{ NO}_3$ and $0.3\text{-}0.4 \text{ mmol}\cdot\text{m}^{-3} \text{ PO}_4$ at the end of April. Values of $8\text{-}9 \text{ mmol}\cdot\text{m}^{-3} \text{ NO}_3$ are normal in March so obviously the spring phytoplankton bloom has started already in mid April and consumed part of the nutrients. Fig. 3a, b show NO_3 and PO_4 concentrations. The lowest concentrations are found at the end of May in the upper layers, less than

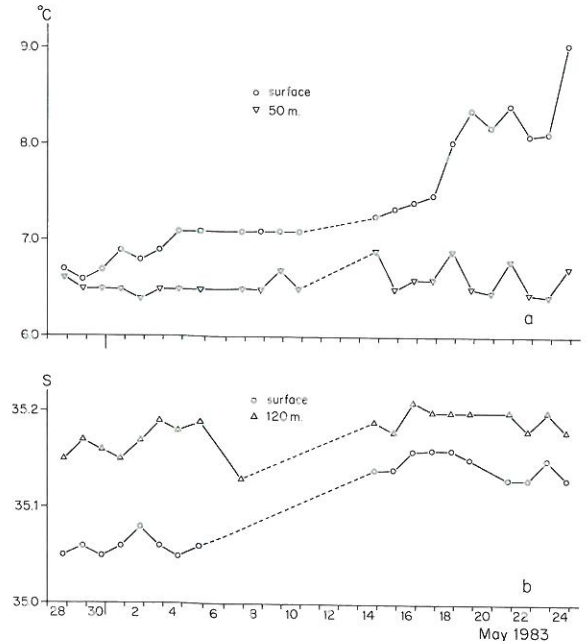


Fig. 2. a. Temperature at the surface and at 50 m depth near the drifter. b. Salinity at the surface and at 120 m depth near the drifter.

$1 \text{ mmol}\cdot\text{m}^{-3} \text{ NO}_3$ in the upper 20 m water layer after 14 May, and less than $0.15 \text{ mmol}\cdot\text{m}^{-3} \text{ PO}_4$ after 19 May in the upper 15 m. From the decrease of nitrate in the surface water, using the Redfield ratio, the production of organic matter has been calculated (see 3.6.2.).

3.2. OXYGEN REGIME

Fig. 3c shows % oxygen saturation. Supersaturation occurred to a depth of 50 to 70 m; a slight undersaturation in deeper layers indicates a surplus of respiration. Apparently oxygen produced by photosynthesis outweighs the oxygen consumption in the upper layers, causing the increased oxygen concentrations. The escape of oxygen to the atmosphere continues as long as the supersaturation at the surface exists. In the discussion we will compute the magnitude of the oxygen escape with the flux equation (KANWISHER, 1963; TIJSSSEN & EIJGENRAAM, 1982).

Assuming vertically homogeneous oxygen conditions close to 100% at the end of the winter, the undersaturation in the lower 50-120 m means that part of the organic matter produced in the photic layer has been respired in the deep water.

Measurement of *in situ*- diurnal oxygen concentrations have been shown to be a valuable estimate of primary production in the Southern Bight of the North Sea in a spring bloom (TIJSSSEN & EIJGENRAAM, 1982) and in the spring-summer period in the Oyster Grounds (TIJSSSEN & WETSTEYN, 1984). Although variability

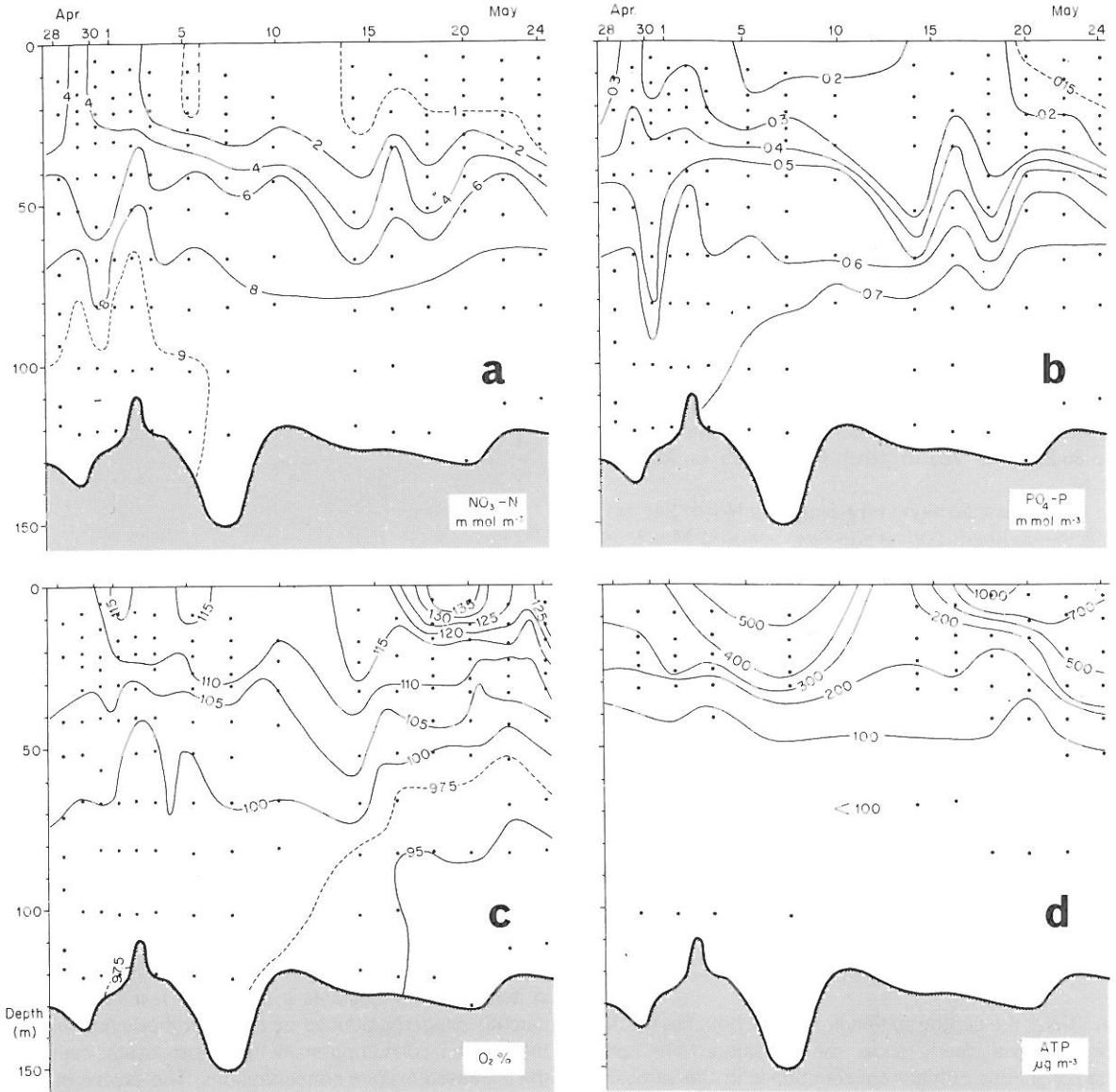


Fig. 3. a. Vertical distribution of $\text{NO}_3\text{-N}$ ($\text{mmol}\cdot\text{m}^{-3}$) in the water mass marked by the drifter during May 1983. b. Vertical distribution of $\text{PO}_4\text{-P}$ ($\text{mmol}\cdot\text{m}^{-3}$). c. Vertical distribution of oxygen saturation percentages. d. Vertical distribution of microbial biomass expressed in ATP ($\mu\text{g}\cdot\text{m}^{-3}$).

sometimes disturbs the estimates. We tried to apply this method during two 48 h periods. In such a period 10 consecutive vertical casts were taken within a few hundred meters around the drogue and integrated oxygen values per m^2 calculated. The attempts were unsuccessful probably due to strong variability in the horizontal (and vertical) plane. A series of simultaneous horizontal surveys, with sampling distances of 300-600 m, taken at sunrise and sunset at a standard depth of 15 m served to quantify this variability (see 3.5). Eleven duplicate

samples were taken on each leg and mean oxygen concentrations computed for these 2.5 - 6 km legs. In four out of six cases diurnal variations were observed. In two light periods +4 and +6 $\text{mmol}\cdot\text{m}^{-3}$ and in two night periods -5 and -6 $\text{mmol}\cdot\text{m}^{-3}$ were measured. These values are in the same range as found by the oxygen incubation primary production measurements (GIESKES & KRAAY, 1986). However these single depth values do not allow an estimation of the integrated primary production.

TABLE 2

ATP concentrations in surface water of various regions. (From VOSJAN, 1988; VOSJAN & NIEUWLAND, 1987; VOSJAN *et al.*, 1987 and from unpublished observations).

Fladengronds, spring	1000 $\mu\text{g}\cdot\text{m}^{-3}$
Off the coast of Texel, summer	5000 $\mu\text{g}\cdot\text{m}^{-3}$
Dutch Wadden Sea, summer	6000 $\mu\text{g}\cdot\text{m}^{-3}$
Antarctic regions, winter	200 $\mu\text{g}\cdot\text{m}^{-3}$
Antarctic regions, summer	1000 $\mu\text{g}\cdot\text{m}^{-3}$
Indonesian waters, NW monsoon	150 $\mu\text{g}\cdot\text{m}^{-3}$
Indonesian waters, SE monsoon	400 $\mu\text{g}\cdot\text{m}^{-3}$

3.3. DISTRIBUTION OF BIOMASS

In Fig. 3 d the ATP concentrations in $\mu\text{g}\cdot\text{m}^{-3}$ have been given. In general it shows the highest concentrations in the upper 10 meters and below 50 m depth the ATP content is low (below $100 \mu\text{g}\cdot\text{m}^{-3}$). Highest surface values were observed on 5 and 19 May. Highest oxygen concentrations were found at the same places (Fig. 3c); this suggests also highest primary production.

Surface values of ATP concentrations of several hundreds to more than $1000 \mu\text{g}\cdot\text{m}^{-3}$ have been found. In

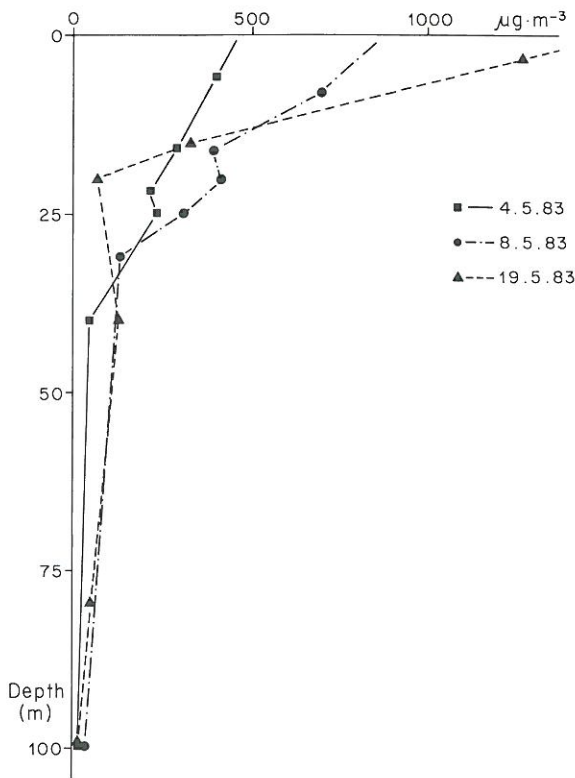


Fig. 4. Vertical distribution of ATP in $\mu\text{g}\cdot\text{m}^{-3}$ on 4, 8 and 19 May 1983 plotted against depth in m.

Table 2 we compare these values with values measured with exact the same method in other regions.

From the Table 2 can be concluded that the Flex box area have biomass values as in a productive area. The values are lower than found in eutrophicated areas as the Dutch Wadden Sea and higher than found in regions of moderate productivity as Indonesian waters during the SE monsoon.

The vertical distribution of ATP in $\mu\text{g}\cdot\text{m}^{-3}$ is given in Fig. 4. Integration of the vertical profiles gives the ATP per m^2 ; the values of 37 vertical profiles show a high variance (Fig. 5), and no clear trend of increasing biomass during May. Such a trend would be expected during this period. Neither did CADÉE (1986) find an increase in particular organic carbon. The mean value and standard deviation of all the observed profiles is $20.4 [\pm] 6 \text{ mg ATP}\cdot\text{m}^{-2}$ ($N=37$), so the standard error of the mean is $1 \text{ mg}\cdot\text{m}^{-2}$. Assuming a C/ATP ratio of 250 gives a biomass in the water column of $5 \text{ gC}\cdot\text{m}^{-2}$.

The ATP concentration in the upper 13 cm of two undisturbed sediment cores was measured. The vertical distribution is shown in Fig. 6. Highest concentrations of about $100 \text{ ng ATP}\cdot\text{cm}^{-3}$ are found in the surface layer, quickly decreasing to a concentration of a few ng per cm^3 at a depth of 10 cm. Comparison of Fig. 6 with Fig. 4 (mind the units) shows in the sediment surface values of $100 \text{ ng}\cdot\text{cm}^{-3}$ and in the water surface about $1 \text{ ng}\cdot\text{cm}^{-3}$; thus the sediment surface is rich in biomass. Integration of the sediment profiles values yields about $4.5 \text{ mg ATP}\cdot\text{m}^{-2}$, compared with the water column value of $20 \text{ mg}\cdot\text{m}^{-2}$ this is about one fifth. So the 10 cm sediment layer is very rich in biomass compared with the 125 m watercolumn. Using the ratio 250 a biomass of small organisms of $1.1 \text{ gC}\cdot\text{m}^{-2}$ is found in the sediment. In the Dutch Wadden Sea values between 0.34 and $6.8 \text{ gC}\cdot\text{m}^{-2}$ were found in september (VOSJAN, 1987). DE WILDE *et al.*, (1986) described a macrofauna biomass of $10.7 \text{ g AFDW}\cdot\text{m}^{-2} = 4.3 \text{ gC}\cdot\text{m}^{-2}$ for the Fladen Ground Area. This is in comparison with the microorganisms biomass remarkable high. Higher in the food chain we normally expect lower biomasses.

3.4. RESPIRATION ACTIVITY

In situ oxygen respiration rates (R) were obtained, for two casts, by incubating samples in 2 l bottles during 24 h in darkness. The bottles were stored at *in situ* temperature levels. Oxygen loss was determined by high precision Winkler titration. The electron transport system activities (ETS-activity) in the original samples were determined and the observed profiles for both measurements are given in Fig. 7a + 7b. The samples served to calculate a calibration value for the ratio ETS/R of $4.3 [\pm] 1.4 (N=9)$. In incubation experiments in July in coastal waters we found values of $4.1 [\pm]$

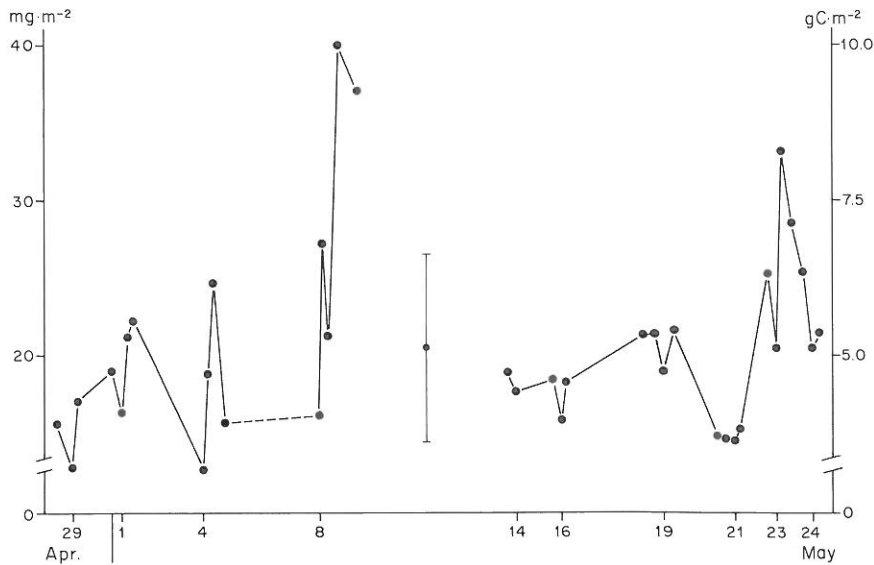


Fig. 5. ATP in $\text{mg} \cdot \text{m}^{-2}$ or biomass in $\text{g C} \cdot \text{m}^{-2}$, integrated over the whole water column during the cruise. In the centre of the figure the mean value and the standard deviation, indicated by a vertical bar, is plotted.

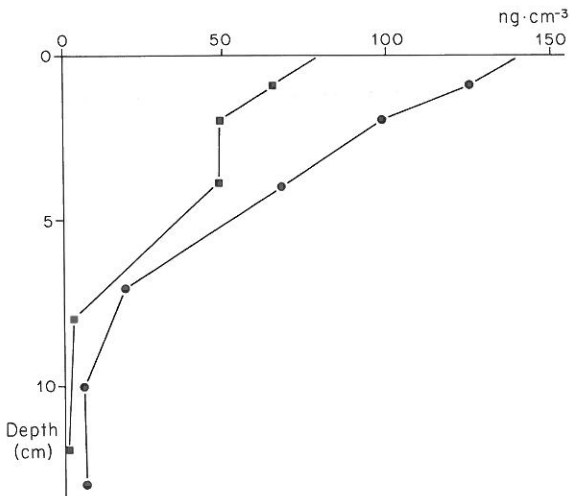


Fig. 6. ATP content of two sediment cores, in $\text{ng} \cdot \text{cm}^{-3}$ plotted against depth in cm.

1.3 (unpublished results) and in Indonesian waters 3.1 (VOSJAN & NIEUWLAND, 1987; TIJSSSEN *et al.*, 1990 in press).

Maximum activity is observed in the upper ten meters and the activity decreases quickly to thirty meter depth. In the surface layers this respiration is executed for a large part by the phytoplankton; it consists of active producing primary producers, as can be concluded from the oversaturation of oxygen.

In Fig. 8 the respiration activity at incubation

temperature and at *in situ* temperature are represented. We measured 37 profiles and found that in the surface layer of the Flex area the ETS-activity at *in situ* temperature is several hundreds to thousand $\text{nmol} \cdot \text{dm}^{-3} \cdot \text{h}^{-1}$.

In Table 3 the ETS-activity in surface waters of various regions is given. The respiration activity in the Flex area is lower than in eutrophicated areas and higher than in regions of moderate productivity.

The real oxygen uptake rates were calculated from the measured ETS activity with the observed ETS/R ratio of 4.3. These respiration rates were converted to carbon units using a $\text{RQ}=1$. For 37 measured profiles the activity was integrated over the water column and expressed as respired carbon per m^2 per day (Fig. 9). Mean and standard deviation were $1.5 [\pm] 0.7 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ($N=37$), which stresses the high variability in respiration activity in the water mass.

In chapter 3.3. we concluded that per m^2 about one fifth of the amount of biomass of the water column was found in the sediment. If the activities per biomass are the same in the sediment as in the water column the respiration must be about $1.5 / 5 = 0.3 \text{ gC} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. *In situ* bell-jar experiments (DE WILDE *et al.*, 1986) showed an average carbon demand of $0.29 \text{ g m}^{-2} \cdot \text{d}^{-1}$, in the same area during the same period. This is in agreement with our calculated respiration rate for the sediment.

3.5. SPATIAL VARIABILITY

As mentioned before, oxygen variability was studied as

part of the attempts to detect diurnal oxygen variations. Therefore small N-S surveys away from the drogue were made. The results of these surveys and of two larger scale surveys of 18 km are in the Table 4. For a better comparison with variability in ETS-activity, ATP and POC, the oxygen variability percentages (Ster % in Table 4) are not expressed as a percentage of the actual [O₂], but as a percentage of the actual [O₂] minus the equilibrium [O₂], as the equilibrium [O₂] is also present in a system without any biological activity.

The short surveys were done in one hour time, with a mean length of 4.2 km, (the distance between samples was in the range 250- 600 m.), or were done in 2 hours over 18 km (sample distance about 3500 m). There seems to be a tendency of higher variability with increasing length scale, and for W-E compared to N-S, but the number of 18 km surveys is too small to prove such effects. Results of one of the short surveys,

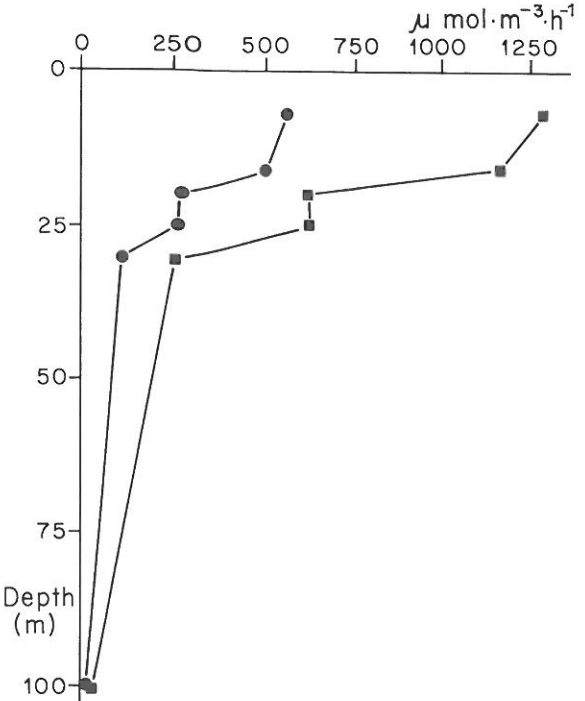


Fig. 8. Vertical distribution of ETS-activity at *in situ* temperatures (o) and at incubation (20°C) temperature (□) in $\mu\text{mol}\cdot\text{m}^{-3}\cdot\text{h}^{-1}$. The ETS-activity at *in situ* temperature is calculated with the Arrhenius equation, in which a during the cruise estimated activation energy of $10.5\pm 1.8 \text{ Kcal}\cdot\text{mol}^{-1}$ is used.

representative in variability, are given in Fig. 10. In two 18 km surveys simultaneous sampling for POC, ATP and ETS-activity was performed (Fig. 11). All parameters showed strong variability, up to 87% in ETS-activity. The variability in the W-E legs seems to be higher than in the N-S legs. Also is in the W-E leg the high ETS activity correlated with a low oxygen content.

TABLE 3

ETS-activity at *in situ* temperature in surface waters. (From VOSJAN, 1988; VOSJAN & NIEUWLAND, 1987 and unpublished data)

Fladenground, spring	<1000 $\text{nmol}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}$
Off the coast of Texel, summer	5000 $\text{nmol}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}$
Clear Channel water, North Sea	100 $\text{nmol}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}$
Dutch Wadden Sea, summer	6000 $\text{nmol}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}$
Indonesian Seas	200 $\text{nmol}\cdot\text{dm}^{-3}\cdot\text{h}^{-1}$

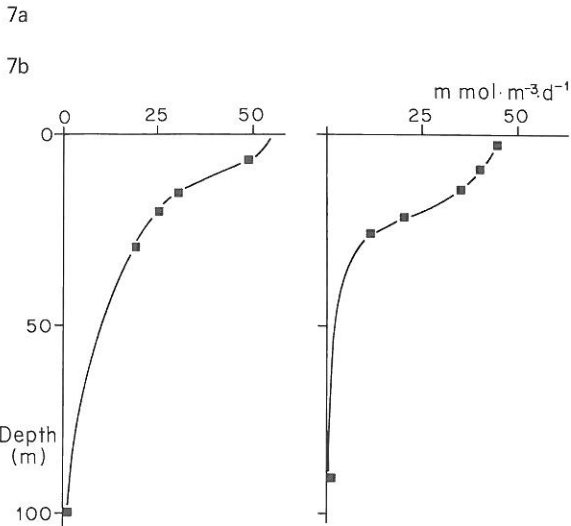
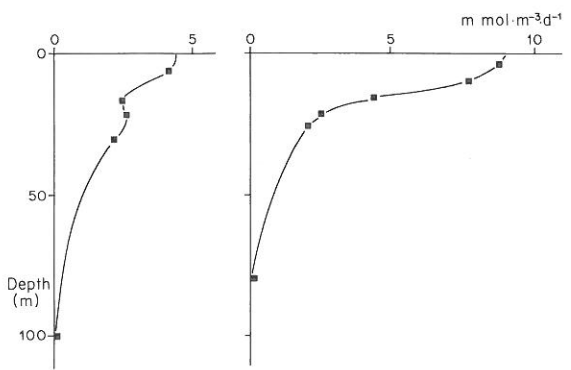


Fig. 7. a. Vertical distribution of Oxygen uptake rate measured in dark incubation experiments ($\text{mmol}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$). b. ETS-activity of the same samples as in Fig. 7a ($\text{mmol}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$).

TABLE 4

Mean horizontal (O_2) variability on surveys at 15 m depth in the Fladen Ground area, May 1983. (N= number of duplicate samples).

Data/time	Temp +Stdv	Sal. +Stdv	Oxygen Conc. +Stdv+Ster	N	Dir.	Lenght km	Remark
GMT			mmol·m ⁻³ %				
30/4 20.20	6.64 0.03	36.03 0.00	333 4 12	11	N-S	6	Fig. 10
1/5 03.30	6.63 0.03	35.03 0.00	328 3 10	11	N-S	5	
1/5 21.00	6.66 0.04	35.03 0.00	334 8 23	11	N-S	5	
2/5 03.15	6.79 0.04	35.04 0.00	343 3 6	11	S-N	2.5	
15/5 21.30	7.36 0.03	35.03 0.01	346 3 7	6	S-N	18	
16/5 00	7.36 0.03	35.13 0.01	338 8 21	6	W-E	18	
16/5 03.10	7.36 0.02	35.14 0.00	336 2 5	11	N-S	2.8	
16/5 20.40	7.40 0.02	35.14 0.00	340 3.5 8	11	N-S	4	
17/5 01.50	7.40 0.02	35.14 0.00	340 5 13	11	N-S	5	
25/5 03.30	7.84 0.42	35.11 0.02	345 17 38	6	E-W	18	Fig. 11
25/5 05.50	8.18 0.38	35.11 0.02	354 7 13	6	S-N	18	Fig. 11

These studies illustrate the high variability in the different parameters. This variability is not due to inaccuracy in the analytical methods, but the ecosystem, on a small scale in time and space, has a high degree of patchiness of living material with consequences for variability in concentrations of nutrients and oxygen. From this variability studies we conclude that it is very difficult to give exact values for productivity in time over large areas. With the large number of observations made in one watermass during one month we shall try

nevertheless to make some budget calculations for the area.

3.6. OXYGEN AND CARBON BUDGET CALCULATIONS

In combination with data from CADÉE, 1986; FRANSZ & DIEL, 1986; GIESKES & KRAAY, 1986; DE WILDE *et al.*, 1986; our results were used to calculations and comparisons on:

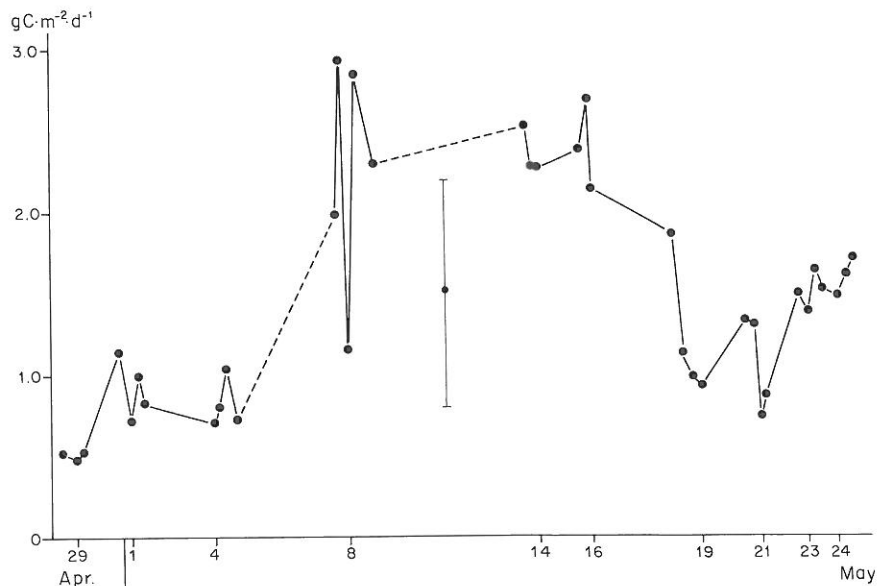


Fig. 9. Respiration rate integrated over the whole watercolumn in $gC \cdot m^{-2} \cdot d^{-1}$ during the cruise, mean value (1.5) with variation is indicated.

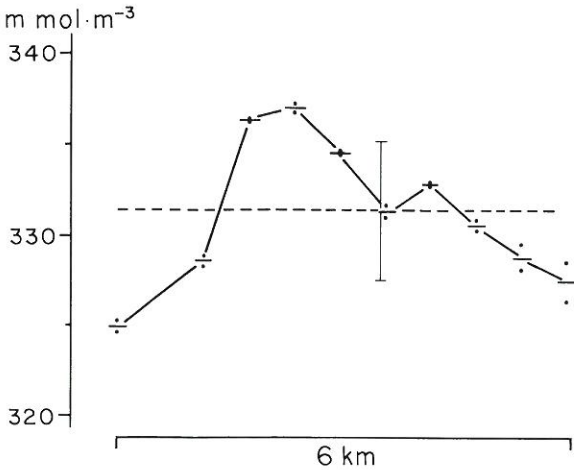


Fig. 10. Oxygen concentration variations within a distance of 6 km at a depth of 15 m. Duplicates show the high precision of the observations. Mean (—) with variation is indicated. (Survey of 30 April, see also Table 4).

3.6.1. OXYGEN FLUX TO THE ATMOSPHERE

The equation for gasexchange with the atmosphere has already been formulated by KANWISHER (1963) and is still used in open ocean studies (SMETHIE *et al.*, 1985).

$$F = k \cdot ([O_2]_{act} - [O_2]_{eq}) \text{ or } F = k \cdot [O_2]_{eq} \cdot \{O_2\% / 100 - 1\}$$

Where in F is the flux in $mmol \cdot m^{-2} \cdot d^{-1}$, k is the piston velocity ($m \cdot d^{-1}$), $[O_2]_{act}$ the surface oxygen concentration and $[O_2]_{eq}$ the equilibrium concentration at ambient temperature and salinity.

The mean surface $O_2\%$ for the whole period was 119%. During the TTO-TAS study mean wind velocity was $7.2 m \cdot s^{-1}$, slightly lower than during this study and a mean k for Radon was determined of $3.6 m \cdot d^{-1}$. The equivalent k for O_2 must be about 30% higher but we take the Rn value here as a minimum estimate. Total flux for the 27 days period is then $5.5 mol O_2$ ($3.6 \times 0.19 \times 300 \times 27 mmol$) or $175 g O_2 \cdot m^{-2}$, (equivalent to $66 g C \cdot m^{-2}$ organic matter production). Part of the oxygen content in the water is consumed in the layer below 50 m where undersaturation is present. This amount, assuming a 3% decrease in a month period over the 50-120 m layer can be estimated to be $0.62 mol O_2$ ($= 20 g O_2 \cdot m^{-2}$, equivalent to $7.5 g C \cdot m^{-2}$). Therefore net oxygen production is $155 g O_2 \cdot m^{-2}$ (equivalent to $58.5 g C \cdot m^{-2}$).

This creates a major problem in the oxygen-carbon budget, because we fail to find where the large amount of produced carbon shows up in the system. It is clearly not present in the POC part, nor is it sedimented; arbitrarily we assume it in the DOC pool.

3.6.2. NET 'REDFIELD' PRODUCTION DURING OUR STUDY

WEICHAERT (1980) calculated from CO_2 and PO_4 concentration decreases a net community production of $19 g C \cdot m^{-2}$ in 10 days in the Flex Box area at the end of April in 1976. He observed an uptake ratio in the phytoplankton of $\Delta C : \Delta N : \Delta Si : \Delta P = 120 : 19 : 9 : 1$. We observed a NO_3 decrease from 4 to $0.8 mmol \cdot m^{-3}$ over the 0-25 m layer. Using the C:N ratio from WEICHAERT (1980) a total carbon uptake of $0.48 mol \cdot m^{-2}$ is

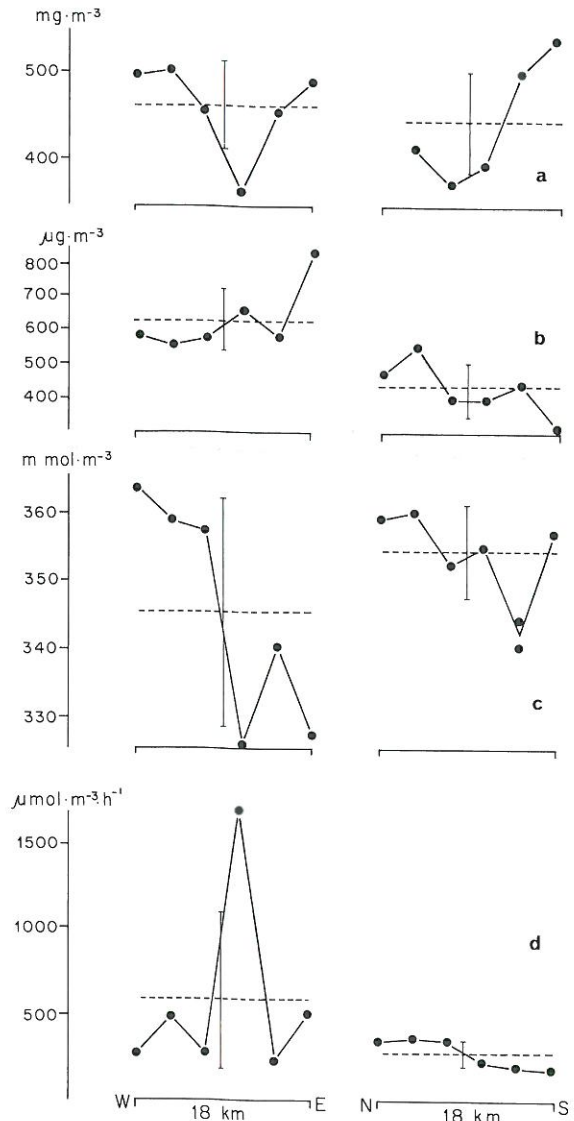


Fig. 11. Variability in a. POC, b. ATP, c. oxygen concentration and d. ETS activity over a distance of 18 km in a W-E transect and in a N-S transect. Mean value (—) and standard deviation (vertical bar) is shown. (Survey of 25 May, see also Table 4).

calculated ($5.8 \text{ g C}\cdot\text{m}^{-2}$ or $31 \text{ g O}_2\cdot\text{m}^{-2}$). Apparently the large carbon production computed from the oxygen flux must have a very high C/N ratio i.o.w. consists for the greater part of carbohydrates or lipids.

3.6.3. BENTHIC FAUNA OXYGEN CONSUMPTION

DE WILDE *et al.* (1986) measured the *in situ* oxygen consumption of the benthic fauna with an automated bell jar equipment at 8 locations during REFLEX. The mean oxygen consumption was $1 \text{ mmol O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. Summed for the whole 27 days period this amounts to 0.65 mol O_2 ($21 \text{ gO}_2\cdot\text{m}^{-2}$) and this matches nicely the calculated oxygen loss (see 3.6.1.) in the water column below 50 m.

3.6.4. SEDIMENTATION RATE

CADÉE (1986) estimated sedimentation rates with floating sediment traps at three depths (40 m, 65 and 70 m) during eight 24 h periods. He observed that 0.1 to 1% of the total POC present in the euphotic layer sedimented per day ($18.8[\pm] 10 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). For the whole period this is $507 \text{ mgC}\cdot\text{m}^{-2}$ ($42 \text{ mmolC}\cdot\text{m}^{-2}$, equivalent to max $84 \text{ mmol O}_2\cdot\text{m}^{-2}$). This is only 13% of the amount of carbon needed to feed the benthic fauna (see 3.6.3).

3.6.5. GROSS PRIMARY PRODUCTION

GIESKES & KRAAY (1986) measured primary production by the oxygen and C-14 method and found values up to $3 \text{ gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (between 14 and 18 May), and also lower values at other times ($< 0.5 \text{ gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). For the whole period the primary production was $1.56 [\pm] 1 \text{ gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ($N=8$). From our oxygen flux calculation follows, that the net ecosystem production must

be at least $2.4 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ while the respiration of microorganisms in the system is $1.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, so gross production must be at least $3.9 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$.

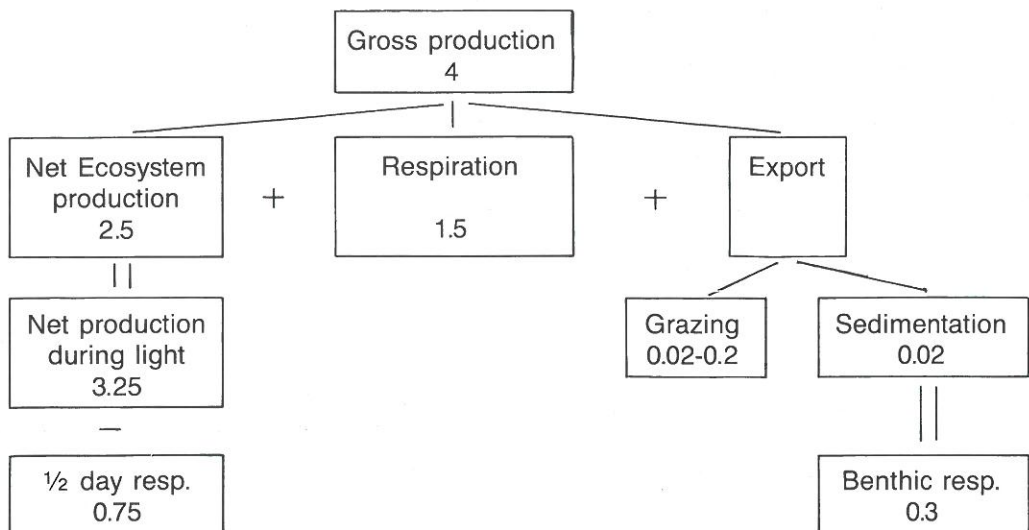
3.6.6. ZOOPLANKTON

FRANSZ & DIEL (1986) studied the secondary production by *Calanus* and found a total carbon production of 1.29 g m^{-2} in 27 days, or $0.044 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. This is less than 2% of the net production. From measurements on grazing during Reflex it is known that less than 10 % of the primary production is used by zooplankton (pers. comm. Baars), so for the carbon budget this factor plays a minor role.

3.6.7. CARBON BUDGET MODEL

The above discussed values in $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ have been summarized in a budget scheme.

In this scheme the observed values for net ecosystem production are larger than $2.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (see 3.6.1), the respiration larger than 1.5 (see 3.4 and 3.6.5) and benthic respiration about 0.3 (see 3.4 and 3.6.3). So gross production (net ecosystem prod + respiration) must be larger than 4. The net ecosystem production is equal with the net production during the light period minus the respiration during the night (dark) period, so the net production is $3.25 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. According mentioned Reflex literature the grazing is between 0.04 to 0.2 (see 3.6.6), the sedimentation about 0.02 (see 3.6.4) and the gross primary production $1.5 \text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (see 3.6.5). So the budget scheme does not fit with the measurements. High variability of observations in time and space and perhaps inadequate sampling techniques in the patchy waters makes it difficult to get a fitting budget. The discrepancies in primary production values obtained by the C-14 and ox-



xygen methods also can be a matter of methodology. And the observed low sedimentation rate in comparison with the high respiration of the benthos raise the question of how the benthos is fed. During this cruise in May there was not enough sedimentation of organic matter to explain the high benthic respiration. DAVIES & PAYNE (1984) reported a very much higher sedimentation in the same area during Flex' 76. So also here the temporal variability in sedimentation may keep us from making a fitting budget.

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