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Respiration and biochemical composition of sedimenting organic matter during summer in the Barents Sea

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Abstract—Sedimentation of particulate carbon and nitrogen, pigments (fluorometric and HPLC analysis) as well as the activity of the respiratory electron transport system in sedimented matter were studied with unpoisoned, short-term deployed sediment traps during June in the central Barents Sea. The vertical flux of sedimenting material and its biochemical composition in the central Barents Sea was different during summer compared to spring with decreased flux of organic matter and decreased relative supplies of particulate nitrogen, but increased phaeopigment concentrations. The summer situation in the Barents Sea is characterized by recycling of the bulk of the suspended matter in the upper layers, a comparatively small loss of suspended biomass, but high sinking rates of some few, large particles, presumed to be faecal pellets. Respiration calculated as a daily loss rate of carbon in the sedimented material was on average only 1.4% day^{-1}. Loss was strongly temperature dependent. At *in situ* temperatures >5°C, it is necessary to estimate turnover rates for sedimenting carbon in non-poisoned traps for an accurate elemental budget of a system and for interpretation of estimates from long-term trap deployments.

INTRODUCTION

THE downwards flux of particulate organic matter from the surface of the ocean depends on the physical structure of the water column (e.g. stratification, turbulence, light), the physical properties of the particulate matter itself and the prevailing planktonic food chain (type of phytoplankton and zooplankton organisms, microbial loop, etc). During spring and early summer, phytoplankton in subpolar and polar waters of the Nordic seas are dominated by large species of diatoms and colonies of the prymnophycean algae *Phaeocystis pouchetii* (SKJOLDAL and REY, 1989; WASSMANN *et al.*, 1990). The impact of herbivorous grazers on the development of the spring phytoplankton bloom in coastal areas and shelf seas is often limited by a significant time-lag in zooplankton development (HEINRICH, 1962; PEINERT *et al.*, 1989). As a result, large amounts of suspended biomass may settle out of the euphotic zone during a senescent phase of the phytoplankton spring bloom (SMETACEK *et al.*, 1984; BODUNGEN *et al.*, 1986; WASSMANN *et al.*, 1991). One consequence of this

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development is an impoverished euphotic layer with respect to seston and nutrients during the summer season.

Sedimentation of a large proportion of biomass provided by the spring phytoplankton bloom determines the onset of the summer period of lower pelagic productivity in coastal areas and shelf seas. During summer loss of organic material due to sedimentation out of the euphotic zone is balanced by the close coupling of primary production and heterotrophic breakdown of organic matter (i.e. a dominance of regenerated production), giving rise to small loss rates of particulate organic and inorganic material. The activities of the various size categories of grazers and a well-structured microbial community may give rise to extensive planktonic respiration rates which are of far greater relative significance during summer compared to spring as demonstrated by HARGRAVE and PHILLIPS (1989) for a temperate marine bay.

During the summer period many boreal off-shore regions and large parts of the Arctic oceans experience "blue-water" conditions comparable to those of oligotrophic oceans, i.e. periods of time characterized by low phytoplankton biomass, low nutrient concentrations, a diverse and relatively rich zooplankton and microbial community as well as extensive recycling of suspended biomass and nutrients (SAKSHAUG and HOLM-HANSEN, 1984; PEINERT *et al.*, 1989; SMITH and SCHNACK-SCHIEL, 1990). This is also true for the Barents Sea, a relatively shallow, continental shelf sea north of Norway and Russia, whose northern realm is periodically covered by sea-ice (REY and LOENG, 1985; SAKSHAUG and SKJOLDAL, 1989). During summer, nitrate concentrations are usually below detection limits ($<0.1\,\mu M$) and chlorophyll *a* concentrations are $<2\,\mu g\,l^{-1}$ in the euphotic zone (REY *et al.*, 1987). Grazing by the dominant herbivores, i.e. copepods, can be substantial (TANDE and BÅMSTEDT, 1985; SKJOLDAL *et al.*, 1987) and vertical flux is usually <100 mg C $m^{-2}\,day^{-1}$ (WASSMANN, 1989).

While primary production measurements in oceanic environments are numerous, estimations of turn-over times of organic matter in the water column are rare (for an overview, see WILLIAMS, 1984). This is also true for direct measurements of the decay rates of sedimenting particles (HARGRAVE, 1978; ISEKI *et al.*, 1980; LORENZEN *et al.*, 1983; HEISKANEN, 1987; HARGRAVE and PHILLIPS, 1989). We present here data on the vertical flux of sedimentary matter, its biochemical composition and respiration in the Barents Sea during summer. We estimate turnover rates for the sedimenting carbon necessary for an accurate elemental budget of the system and for interpretation of sedimentation estimates during long-term trap deployments.

MATERIALS AND METHODS

The data reported were collected in July 1988 during PRO MARE cruise 15 on board R.V. *G.O. Sars* at two locations [73° 00'N, 31° 15'E (Sta. I) and 75° 00'N, 28° 00'E (Sta. II)] in the central Barents Sea. Both stations were situated in areas dominated by Atlantic water. Standard hydrographic sampling was carried out with a Neil Brown Mk III CTD-profiler mounted with a General Oceanic Rosette Sampler equipped with 5 l Niskin bottles. Sampling depths were selected considering the physical and biological structure of the water column as revealed by profiles of temperature, salinity as well as *in vivo* fluorescence obtained with an *in situ* Q-fluorometer.

Water samples for the analysis of nutrients and suspended pigments were taken at a maximum of 20 depths at the two stations which were 278 and 330 m deep, respectively.

Table 1. *Average daily sedimentation rates of particulate carbon and nitrogen* (PC, PN), *chlorophyll a* (*Chl a*) *and phaeopigment* (*Phaeo*) (mg m^{-2} day^{-1}) *and coefficient of variation* (%) *derived from duplicate traps deployed for about* 3 *days at two stations in the central Barents Sea during July* 1988. *Pigment data are from fluorescence analysis*

Station	Depth (m)	PC	PN	Chl *a*	Phaeo
I	40	118.0±13	13.50±22	0.123±11	0.235± 5
(885)	90	96.6± 9	10.74±12	0.117±20	0.442±15
	150	99.7±13	10.02±14	0.063±18	0.196±16
	200	119.4± 6	12.99± 9	0.069±17	0.333± 9
	250	109.1±11	13.08±18	0.063±23	0.262± 5
II	60	47.7±11	5.01±18	0.024±28	0.050±53
(864)	100	126.4± 7	13.34± 7	0.190±29	0.448±26
	230	95.5±22	9.21±13	0.042±58	0.226±60

Settled particulate matter was collected by measuring with anchored, cylindrical duplicate PVC traps (1.6 m high; H/D ratio of 10) without baffles for about 72 h from 40 to 250 m depth at five and three depths, respectively (Table 1). The trapping efficiency of these traps, e.g. by ^{234}thorium data, is not known. The current regime of this part of the Barents Sea is characterized by moderate to low flow rates. No preservatives were placed in traps which were filled with surface water on deployment. Large swimmers which were removed, if present, with a forceps after visual examination of the filters, represented no problem during analysing the samples. Methods for the analysis of nutrients, particulate carbon and nitrogen (PC, PN) and chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo)—fluorometric determination—are described in SKJOLDAL and WASSMANN (1986) and WASSMANN *et al.* (1990). Pigments were also analysed by high pressure liquid chromatography using a fluorescence detector Hitachi U, as described by WASSMANN *et al.* (1990).

The activity of the electron transport system (ETS) was measured in 250 ml samples of trap material. Samples were filtered through GF/F glass fibre filters. The sediment-coated filters were immediately frozen in liquid nitrogen. The ETS assay was performed on the frozen samples, according to PACKARD (1971) with modifications of KENNER and AHMED, (1975). The method has been thoroughly described by PACKARD (1985a,b) and only a short outline will be given here.

Frozen filters were mixed with 5 ml of Na_2HPO_3–KH_2PO_3 buffer (pH = 8) containing Mg and a detergent (Triton X-100) and ground with a tissue homogenizer. One ml aliquots of the homogenate were used for the assay. Two assays and a control were analysed per sample. A substrate containing an excess of electron donors, NADH, NADPH and succinate were added to the assays. The controls were added a "blank substrate" without the donors. The tetrazolium salt INT was added to both assays and controls. The electron transferred from the donors through the ETS reduce the INT to formazan, during fixed time incubation (15 min) in a thermostated water bath at constant temperature at 10°C. The experimental conditions were as described in MARTINEZ (1991). The amount of formazan evolved is proportional to the reducing activity of the ETS present in the homogenate. The optical density of formazan was measured spectrophotometrically at 490 nm. Readings were taken at 750 nm to correct for turbidity. Optical

Table 2. Various ratios characterizing the biochemical composition of sedimented organic matter. Pigments data are based on HPLC analysis

Station	Depth (m)	PN/PC (a/a)	PC/Chl *a* (w/w)	Chl *a* Phaeo (w/w)	PC/Phaeo (w/w)
I	40	0.098	959	0.55	502
	90	0.095	826	0.26	218
	150	0.086	1583	0.11	509
	200	0.093	1730	0.08	359
	250	0.103	1732	0.09	416
II	60	0.090	1988	1.25	954
	100	0.090	665	0.39	282
	230	0.083	2273	0.17	423

densities of the controls were subtracted to correct for other compounds in the samples (i.e. pigments).

The ETS activity at the assay temperature was calculated according to the equation

$$\text{ETS (ml } O_2 l^{-1} h^{-1}) = [60\ S\ H\ COD_{(490)}]/1.42\ V\ t\ T,$$

where:

60 = minute-to-hour conversion
H = homogenate volume (approx. 5 ml)
S = final sample volume before reading
COD = corrected optical density
1.42 = experimental factor from formazan to oxygen concentration
V = total initial volume filtered in litres
t = incubation time (15 min)
T = homogenate aliquot taken for the assay.

The activation energy of the enzyme system determined for parallel microplankton samples was $E_a = 11.5 \pm 0.6$ kcal mol^{-1} (47.9 kJ mol^{-1}) (MARTINEZ, 1991), and this value was also used here to correct for *in situ* temperature, using the Arrhenius equation

$$\text{ETS } (\textit{in situ}) = \text{ETS (10°C) } e^{-[-E_a/R(1/T_1 - 1/T_2)]},$$

Where E_a is the activation energy, R the gas constant (= 8.31 J mol^{-1} K^{-1}, or 1.99 cal mol^{-1} K^{-1}), T_1 the *in situ* and T_2 the assay temperature in K.

The measured ETS activity was converted to mg C m^{-2} day^{-1} (Table 2) taking into account the total volume collected in the trap at the end of the exposure, the collecting area of the trap and using a C/O respiration quotient of 1. The rates represent the average of those obtained on samples from both cylinders of the traps. No significant differences were found between duplicates. The approach of OLSEN (1963) and WESTRICH and BERNER (1984) were used to calculate instantaneous first-order decay rates (k) for sedimenting organic carbon as the ratio of respiratory carbon loss to daily organic carbon standing stock.

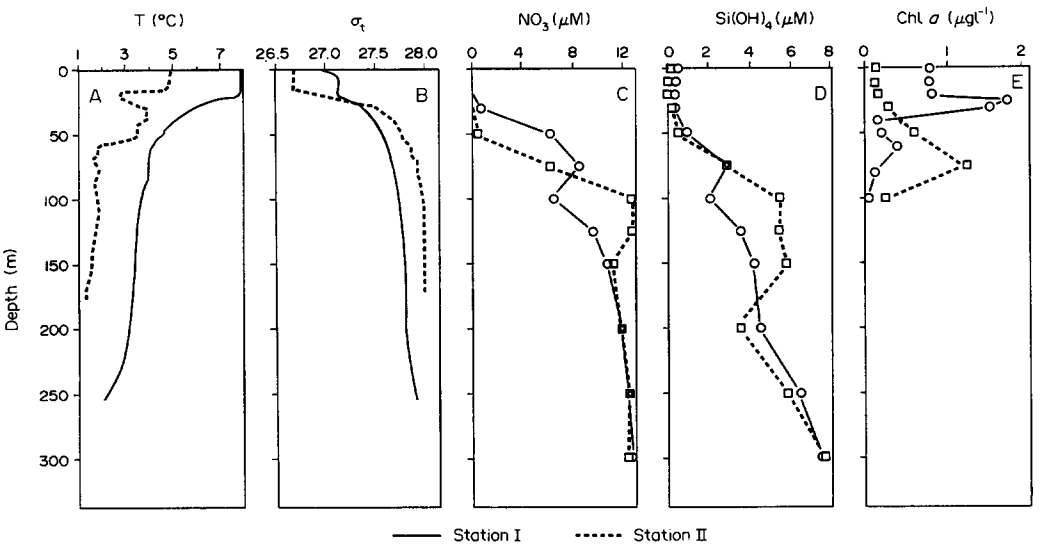

Fig. 1. Vertical profiles of temperature (A), density (B), nitrate (C), silicate (D) and chlorophyll *a* (E) at Stas I (full line) and II (Broken line) during summer in the central Barents Sea.

RESULTS

Hydrography and suspended biomass

The distribution of temperature, density, nutrients and Chl *a* at Stas I and II are shown in Fig. 1. Station I is situated in the southern part of the central Barents Sea which is rarely covered by sea ice and is characterized by warm Atlantic water and a moderately stratified surface layer about 20 m deep during summer [Fig. 1(A),(B)]. Station II is situated in the central Barents Sea which is usually covered by sea ice until May–June and characterized by cooled Atlantic water below a strongly stratified surface layer about 20 m deep [Fig. 1(A),(B)]. Stratification is due to solar radiation at Sta. I, but mainly due to melting sea ice at Sta. II. Nutrient depletion in the euphotic zone of both stations was significant, a typical situation during July in the central Barents Sea [Fig. 1(C),(D)]. Station I had a higher and less pronounced nitracline than Sta. II, probably due to less stratification and enhanced diffusion into the mixed layer. Silicate concentrations in the mixed layer were well above zero at Sta. I and just above detection limit at Sta. II. Compared to Sta. II, silicate concentrations at Sta. I were lower between 75 and 150 m.

No data of ammonia concentrations are available from the present stations. The ammonia concentrations from other stations visited during the cruise in the central Barents Sea were generally high in the upper 100 m of the water column and ranged between 0.2 and 3.7 μM with an average of 1.2 ± 69% ($n = 85$). The maxima were usually found at 50 m depth, just below the euphotic zone.

A typical summer Chl *a* maximum in the lower part of the euphotic zone was found [Fig. 1(E)]. It was situated at about 20 m depth at Sta. I and fairly deep at 70 m at Sta. II. The Chl *a* maximum was situated well above the nitracline at both stations [Fig. 1(C),(E)]. Despite the differences in the depth distribution of Chl *a*, both stations had similar integrated biomass in the upper 100 m of 51 and 54 mg Chl *a* m^{-2} while phaeopigments

were 19 and 13 mg Phaeo m^{-2} for Stas I and II, respectively. Both stations differed also in their phytoplankton species composition with Sta. II dominated by prymnesiophytes while mostly diatoms were found at Sta. I (M. Vernet, unpublished results).

Sedimentation of particulate organic matter and silicate

PC and PN sedimentation rates at Sta. I were on average about 108 and 12.1 mg m^{-2} day^{-1}, respectively, and showed little variation with depth (Table 1). Chl *a* sedimentation decreased with depth in the upper 90 m and remained low and constant to 250 m while Phaeo sedimentation was more variable.

Station II showed a clear maximum in sedimentation at 100 m, below the chlorophyll maximum (Table 1). Average PC and PN sedimentation rates were 90 and 9.2 mg m^{-2} day^{-1}, respectively. Sedimentation of Chl *a* and Phaeo were similar to Sta. I. The daily loss rates of suspended Chl *a* and Phaeo at about 100 m depth were 0.23 and 0.35 and 2.3 and 3.4% at Stas I and II, respectively.

Biochemical composition of sedimenting organic matter

Various ratios characterizing the biochemical composition of sedimented matter are presented in Table 2. Compared to the Redfield ratio the sedimenting organic matter is clearly depleted for nitrogen as indicated by a low and constant PN/PC ratio (average = 0.092). High PC/Chl *a* ratios (Table 2), about an order of magnitude higher than during spring WASSMANN *et al.* (1990), were measured throughout the water column, with maximum values at depth, indicating that little fresh phytoplankton was sinking from the upper part of the water column during time of trap deployment. Minimum values of PC/Chl *a* were measured in traps situated below the chlorophyll maxima, at approximately 100 m. The ratio of Chl *a*/Phaeo was fairly high in the upper 100 m of the water column, similar to spring values (WASSMANN *et al.*, 1990), and was twice as high at Sta. II as compared to Sta. I at any given depth sampled. The ratio of PC/Phaeo did not show any pattern of distribution with depth, with average values 5–10 times higher than in spring. Similar to the PC/Chl *a* ratio, minimum values were observed in material collected below the chlorophyll maximum.

Respiration of sedimenting organic matter

Table 3 shows the ETS activities at Stas I and II, the daily loss rates as well as the decay times of PC in the traps. The ETS activities ranged between 0.6 and 14.7, with an average of 4.89 mg C m^{-2} day^{-1}. The ETS activities were significantly higher at Sta. I than II, both absolutely and relative to the PC sedimentation rate (Table 3). The ETS activities indicated a maximum at intermediate depths of 100 and 90 m, respectively. This coincides with maximum sedimentation rates at Sta. II, but not at Sta. I. The ETS activity rate at 90 m depth at Sta. I was much higher than the remaining rates (Table 3). The proportion of carbon which is daily respired in the trapped material ranged between 0.4 and about 5% with an average of 1.4%.

The relationship between the carbon-specific ETS rate vs *in situ* temperature indicates a significant exponential dependence (Fig. 2), suggesting that the proportion of sedimenting

Table 3. Respiratory ETS *activity of sedimenting organic matter derived from sediment traps at various depths at two stations in the Barents Sea during July. Also shown are the daily loss rates of sedimenting* PC *by respiration* (ETS) *activity/*PC *sedimentation), and the decay time to reach* 95% *of* PC *concentration* (3/k)

Station	Depth (m)	Temperature (°C)	ETS activity (mg C m^{-2} day^{-1})	Daily loss rates (%)	95% decay time (days)
I	40	4.10	4.31± 6% (4)	1.2	250
	90	3.83	14.66± 8% (4)	4.9	61
	150	3.39	4.78±20% (3)	1.6	188
	200	3.12	4.01±10% (4)	1.1	300
	250	2.20	2.35± 7% (4)	0.7	430
II	60	1.80	0.61±16% (4)	0.4	750
	100	1.78	2.38±17% (3)	0.6	500
	230	1.50	1.11±24% (3)	0.4	750

organic carbon consumed in respiratory processes (turn-over rate) is strongly temperature dependent.

Decomposition usually follows an exponential decay and the time to consume 95% of observed levels of organic carbon (95% decay time) is $-\ln(0.5)/k = 3/k$ (OLSEN, 1963). 95% decay times ranged between 60 and 750 days (Table 3).

DISCUSSION

Overall, both stations showed very similar sedimentation rates with numbers comparable to previous results from oligotrophic summer situations in the central Barents Sea (WASSMANN, 1989). The sedimentation rates of PC and Chl *a* out of the euphotic zone during August 1985 were 109 and 0.06 as compared to 97.3 and 0.11 mg m^{-2} day^{-1} in July 1988, respectively. The loss rates of suspended pigments from the euphotic zone indicate

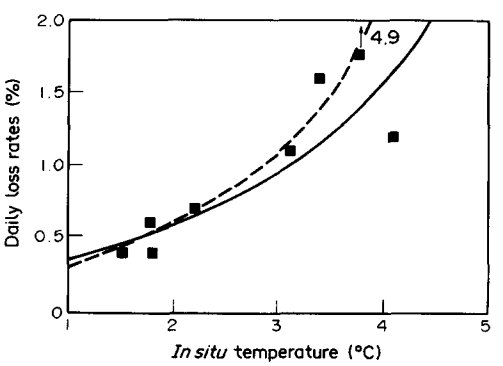

Fig. 2. The daily loss rates of sedimenting PC by respiration (carbon-specific ETS activity) as a function of *in situ* temperature. Best fit to the distribution out of three models is provided by the exponential models $y = 0.21\times10^{(0.217x)}$ ($n = 7$: $r^2 = 0.82$) (full line: daily loss rates at 90 m depth at Sta. I not included) and $y = 0.147\times10^{0.3x)}$ ($n = 8$: $r^2 = 0.71$) broken line: all data included).

efficient recycling of Chl *a* in the upper layers since only about 0.3% of the living phytoplankton biomass was supplied daily to depths >100 m on average. Heterotrophic breakdown of organic matter in the lower part and below the euphotic zone was reflected by maxima and generally high ammonia concentrations (>1.5 μM) in the investigated area. However, for phaeopigments the situation is different with daily loss rates of suspended biomass from the upper layers which are an order of magnitude higher (average: 2.8%). This reflects the significance of larger herbivores for the dynamics of seston in the upper layers during summer and the concomitant sedimentation of rapidly sinking, phaeopigment rich faecal material. Although the maximum of the ETS activity clearly coincided with maxima in phaeopigment fluxes in the sediment traps, there was no significant relationship between both variables. The data seem to indicate that maxima of respiratory activity in traps are related to sinking of macro-zooplankton faecal pellets which might reflect microbial organisms attached to them (SILVER *et al.*,1984; DUCKLOW *et al.*, 1986; TAYLOR *et al.*, 1986).

The sedimented matter at Stas I and II showed similarities in PC and PN content while the pattern of chlorophyll and phaeopigments suggested different mechanisms of formation and/or recycling. The high PC/Chl *a* and PC/Phaeo ratios seem characteristic of summer sedimenting matter and might originate from ingestion by zooplankton of cells with low pigment content (RICHARDSON *et al.*, 1983)). On the other hand, these high ratios might indicate a longer food web where pigments degrade preferentially with respect to carbon, or where a lower proportion of the total grazing originates from herbivory (DOWNS and LORENZEN, 1985). The high Chl *a*/Phaeo ratios in the upper 100 m of the water column at both stations seem to suggest that the sedimenting material is fresh, giving support to the first hypothesis.

The general decrease of the Chl *a*/Phaeo ratio and the increase of PC/Chl *a* (below 100 m) with depth suggests preferential degradation of chlorophyll *a* as the detritus sinks (LORENZEN, *et al.*, 1983). The lower ration of Chl *a*/Phaeo at Sta. I throughout the water column, as compared to Sta. II, seems to originate from seston. The Chl *a*/Phaeo ratios in the suspended matter for the upper 100 m at Sta. I were also about 50% of those at Sta. II (M. Vernet, unpublished results). These differences might originate from phytoplankton (diatoms at Sta. I as opposed to prymnesiophytes at Sta. II) and the grazers associated with them. The high Chl *a*/Phaeo ratio at 60 m at Sta. II (Table 2), combined with low sedimentation rates of both pigments, seem to imply that most of the material collected at the chlorophyll maximum is dominated by living cells.

The ETS activity measured is a potential respiration rate. Actual respiration (R = oxygen consumption rate) should be equal or lower than the ETS activity. Mean ETS/R ratios of about 3 have been reported (PACKARD, 1985a) for microplankton assemblages in temperate zones and in algal cultures. Also in zooplankton in the Barents Sea an ETS/R ratio of 3 has been measured (Falkenhaug and Martinez, unpublished results). However, no comparisons exist for either Polar mixed microplankton populations or sedimenting matter, although there are indications that respiration could be closer to ETS activity in Polar microplankton (Kraay, unpublished results; Martinez, unpublished results). Therefore, we report our ETS activity without conversion, although we can assume that the actual respiration is to be found somewhere between 0.3- and 1-fold of the ETS activity.

The average breakdown rates of organic matter in sediment traps during this study were small compared to rates reported in other studies. In contradiction to the present

investigation all these studies were based on O_2 uptake or CO_2 release of rotated sediment suspensions. HARGRAVE (1978) recorded average breakdown rates ranging from about 14 to 19 mg C m^{-2} day^{-1} in a boreal, marine bay during summer, about 5–7% of the daily carbon sedimentation rate. ISEKI *et al.* (1980) calculated average daily decomposition rates of sedimented carbon at 15°C of 29, 5, 3 and 2% at 10, 20, 30 and 50 m depth, respectively, in a boreal fjord (March–April). These rates reflect the decreasing nutritional quality of the sedimenting organic matter with increasing depth. LORENZEN *et al.*, (1983) encountered average breakdown rates of particulate carbon of about 30% in the upper 900 m of a tropical environment while HEISKANEN (1987) found average carbon breakdown rates in sediment traps of about 10% in a Baltic environment (April–September). Daily carbon loss rates of 1.1–1.4% were recorded by HARGRAVE and PHILLIPS (1989) for detritus in a macrotidal, boreal environment during August. Despite the far higher temperatures in this environment the latter rates are comparable to those calculated for Sta. I (Table 3). However, they are 2–3 times higher than those calculated for Sta. II.

Higher daily losses (Table 3), measured at Sta. I with respect to Sta. II, were associated with lower Chl *a*/Phaeo ratios at the former station (Table 2). Diatom-derived detritus seems to degrade faster than prymnesiophytes. The decrease in daily loss rates with depth in Sta. I could suggest higher microbial activity in the upper water column. It is associated with a higher Chl *a*/Phaeo ratio suggesting that fresher material degrades faster. The same pattern was not observed at Sta. II though, where the Chl *a*/Phaeo ratio still decreased with depth while the daily loss rates were low and constant.

It is obvious that the turnover rates for the sedimenting carbon are significantly different in different investigations. Generally low values found in the present study suggest that microbial decomposition of sedimenting matter inside the traps during short-term, summer deployments in the Barents Sea do not severely underestimate carbon sedimentation rates. An accurate elemental budget and the interpretation of sedimentation estimates during trap deployments in the Barents Sea during summer are, therefore, easily established. However, temperature and the biochemical composition plays a significant role for the breakdown of organic matter in general (PACKARD *et al.*, 1975) and, hence also in sediment traps. This is indicated by high daily loss rates in tropical environments (LORENZEN *et al.*, 1983), but also in boreal environments during summer (HARGRAVE, 1978; ISEKI *et al.*, 1980; HEISKANEN, 1987). The temperature dependence of carbon breakdown rates is evident even in the present study with temperatures variations <2.6°C (Fig. 2). The rapid loss of carbon from sediment traps during deployments longer than 1 week and temperatures >10°C (about 10%) have consequences for all sedimentation measurements [GUNDERSEN and WASSMANN (1990) and references therein]. The *in situ* temperature experience by sediment traps during deployment should be carefully considered. Measures should be taken to prevent decomposition even during short-term deployments by adding preservatives or poisons, especially at high temperatures, or decay rates must be calculated and taken into account when carbon sedimentation rates are determined. [For a general discussion of the role of preservatives and poisons in sediment traps see WASSMANN and HEISKANEN (1988, pp. 188–192), KNAUER and ASPER (1989) and LEE *et al.*, (1991).] Also, variables other than temperature are involved in the relationship between temperature and breakdown rates (Fig. 2) such as the quality and composition of sedimenting organic matter. The results of the present investigation can, thus, not be extrapolated to other seasons, other temperature regimes or environments.

Another, yet generally unresolved problem for the estimation of exact sedimentation

rates, is the impact of zooplankton on the material in the traps (LEE *et al.*, 1988, 1991; KNAUER and ASPER, 1989). Larger zooplankton species were not observed in the samples of the present investigation, but quite abundant in poisoned traps during summer (WASSMANN, 1989). In the absence of preservatives/poisons they have probably swum out of the traps again after feeding and defaecation. Macrozooplankton swimming in and out of unpoisoned, but not poisoned sediment traps, have actually been observed by divers in a subarctic, Norwegian fjord (U. Passow and U. Riebesell, personal communication). The presence of small zooplankters in the sedimented material can hardly be avoided (SILVER *et al.*, 1984; TAYLOR *et al.*, 1986). The electron acceptors of the respiration chain of these organisms could have given rise to increased ETS activity in our samples and might have contributed to the maxima recorded at 90 and 100 m depth at Stas I and II, respectively. Small "swimmers" could possibly be the reason for the high ETS activity at 90 m depth at Sta. I which apparently does not fit well into the distribution of temperature vs breakdown rates (Fig. 2).

C-specific ETS activity of sedimenting PC was within the range of that measured in the suspended PC in the same region and cruise (MARTINEZ, 1991). This, together with the fact that the PC/PN ratio was similar in both suspended and sedimenting matter (PC/PN = 11), average value of the 40–300 m integrated water column, suggest that there is a close relationship between the PC/PN ratio of the particulate organic matter and its metabolic activity. High PC/PN ratios during summer, as in this study, indicate high detrital contribution. This is confirmed by the high PC/Chl *a* ratios in the sedimented, as well as suspended, matter in this region during summer (MARTINEZ, 1991). In contrast, higher (5-fold) C-specific ETS activity has been measured in the suspended particulate matter in the Weddell Sea during spring (MARTINEZ and ESTRADA, 1992), which is in agreement with a lower PC/PN ratio (PC/PN = 6) and a high bacterial-low detrital contribution to organic matter that determine higher respiratory turnover rates.

Assuming a sedimentation rate of 100 mg C m^{-2} day^{-1} at 50 m depth, a daily loss rate of carbon in sediment traps of 2%, an average sinking rate of 10 m day^{-1} of the particles, no consumption of sinking particles by heterotrophic organisms and that chemical degradation is insignificant, as little as 67 mg C m^{-2} day^{-1} would reach a depth of 250 m. This can obviously not be the case in the Barents Sea since carbon sedimentation did not decrease with increasing depth (Table 1). This implies that the sedimentation of carbon-containing particles is much higher than 10 m day^{-1} and that the breakdown rates of these rapidly sinking particles dominating the vertical flux is low. The summer situation is thus characterized by recycling of the bulk organic matter in the upper layers, a comparatively small loss of suspended biomass, but high sinking rates of some few, presumably large particles (CHO and AZAM, 1988). These evaluations add another piece of evidence supporting the idea that the vertical flux during the oligotrophic summer situation in the Barents Sea is likely due to faecal pellets of macrozooplankton.

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