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Pelagic-benthic coupling during the onset of winter in a northern Norwegian fjord. Carbon flow and fate of suspended particulate matter

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ABSTRACT: The distribution of suspended material and sedimentation were investigated in a northern Norwegian fjord for 4 wk during the onset of winter in 1989. Total suspended particles and particulate organic carbon ranged in concentration from ca 1500 to 4000 and 70 to 270 $\mu g\ l^{-1}$, respectively, during the investigation. Concentrations of suspended chlorophyll *a* and pheopigments ranged from ca 0.03 to 0.20 and 0.2 to 0.9 $\mu g\ l^{-1}$, respectively. A decreasing tendency was observed over time for chlorophyll *a*; this was presumably a result of reduced phytoplankton growth due to deteriorating light climate associated with the season. Sedimentation rates for total particulate material and POC ranged from 400 to 8000 and from 25 to 300 mg $m^{-2}\ d^{-1}$, respectively. For chlorophyll *a* and pheopigments these rates were from 25 to 250 and 200 to 2000 $\mu g\ m^{-2}\ d^{-1}$, respectively. The beginning and end of the study period were characterized by unusual features, which were attributed to processes of advection and resuspension of sediments. One consequence of these hydrographic processes is a focusing of sediments to deeper parts of the fjord. A carbon budget showed that only a small fraction (< 0.14 % d^{-1}) of suspended POC was respired by the mesozooplankton, whereas up to ca 5 % of suspended POC was exported via sedimentation. Further, best estimates indicate that ca 36 and 18 % of material sinking out of the upper 30 m and from the entire water column, respectively, were potentially respired by the benthos. Community respiration rates for the benthos were up to almost 1 order of magnitude greater than for the mesozooplankton. The nonrespired sedimented material presumably accumulates in the deeper parts of the fjord and may serve as a food source for enhanced benthic production in spring.

INTRODUCTION

Although relatively few, some studies addressing pelagic (e.g. Bathmann et al. 1990) and benthic (Linke 1992) biology as well as pelagic-benthic coupling (e.g. Wassmann 1984) have been conducted in winter in high-latitude regions. In these and related studies addressing physiological adaptations to high-latitude ecosystems (e.g. Clarke 1987, Rey et al. 1987, Conover & Bedo 1991, Conover & Huntley 1991, Graf & Linke 1992) the importance of large amplitudinal seasonal conditions, i.e. global radiation and temperature, for aquatic systems is evident.

Our knowledge of pelagic-benthic coupling during the transition period from fall to winter is sparse. This is a period of particular interest with respect to the biological response to rapidly worsening conditions for primary production especially in high latitudes. Aside from the decline of pelagic production, physiological adaptations such as diapause by macroplankters (e.g. Davis 1976, Tande 1982, Hirche 1983, Hopkins et al. 1984, Colebrook 1985) and morphological adaptations including resting eggs of crustaceans (Marcus 1987) and phytoplankton resting spores and cysts (Syvertsen 1979) may play special roles in the life cycles of individual taxa. Further, in some open-ocean

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systems, the benthos appears to enter a general phase of dormancy (Graf 1989, Graf & Linke 1992).

In coastal areas, the situation particularly with respect to the benthos is less clear. Macroalgae, progressively dislodged from their littoral and sublittoral habitats by turbulent shoreline hydrography in fall/winter, may provide benthic communities with a prolonged food source after pelagic production has decreased to a minimum. Graf (1987) has suggested that in temperate regions winter-accumulated organic matter may represent a food reserve, the consumption of which is triggered by input of fresh food in the form of sedimenting phytoplankton in spring. How does the input of macrophytic or other nonpelagic food resources in fall/early winter affect pelagic structure, sedimentation and benthic activity in high-latitude marine ecosystems?

We conducted an investigation designed to study the flow of particulate organic carbon between pelagic and benthic components of a high-latitude marine ecosystem during the transition period from fall to winter. The area studied was a fjord in northern Norway. Reported here are results from sediment-trap deployments and studies on suspended particulate material. In addition, an estimate of carbon flow in the ecosystem is presented with particular reference to pelagic and other sources of organic matter compared with rates of mesozooplanktonic and benthic respiration. The possible consequence for the biological regime in the following spring is discussed.

MATERIAL AND METHODS

The investigation was conducted from 9 November to 5 December 1989 at an 80 m deep station in Ramfjorden (69° 33' N, 19° 07' E) near Tromsø, Norway (Fig. 1). Hydrocast samples were collected with Niskin bottles in depths of 0, 10, 30, 50 and 70 m every 3 to 4 d with the exception of one 5 d period between sampling. Subsamples were filtered using precombusted Whatmann GF/F glass-fiber filters for analyses of seston (Lenz 1971), particulate organic material (POM, as ash-free dry weight after combustion at 510 °C for 24 h), chlorophyll *a* and pheopigments using a Turner Design fluorometer and methanol as a solvent (Holm-Hansen et al. 1965), and particulate organic carbon and nitrogen (POC, PON) using a CHN analyzer (model 1106 Carlo Erba). Sedimenting material was collected in intervals of 3 to 4 d (with the exception of one 5 d interval) in depths of 10, 30, 50 and 70 m using paired cylindrical sediment traps (collecting area of 157 cm^2 per pair, height:width ratio of 10:1), each of which was fitted with a single collecting cup containing mercury chloride (0.5 ml saturated $HgCl_2$ solution per 100 ml filtered (0.2 µm) seawater collected at 75 m depth and enriched with sea salt by 3 ‰ to a total of about 37 ‰). Sedimented material was split volumetrically in the laboratory for the same analyses as for hydrocast samples.

For estimates of the loss of suspended POC due to sedimentation, concentrations of suspended POC were integrated over the selected depth range (surface to depth of trap). The mean of integrals from 2 successive sampling dates was used to equate losses due to sedimentation between these dates. Due to missing data on 24 November, the integral of values for pelagic POC for this date was approximated from measurements in 0 and 10 m, whereby a mean of these values was used to represent the missing values at 30, 50 and 70 m.

Mesozooplankton was sampled in vertical hauls from 4 depth ranges (70–50, 50–30, 30–10, 10–0 m) with a 90 µm mesh-sized WP2 net and transferred to 20 l containers with surface seawater. In the laboratory

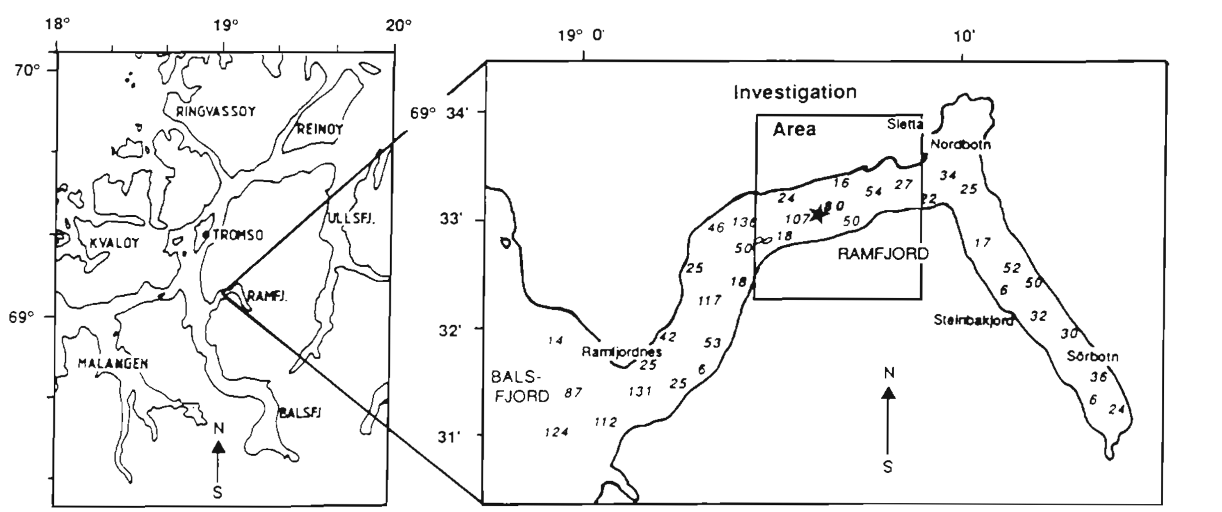

Fig. 1. Investigation area near Tromsø, northern Norway. ★ indicates sampling site in Ramfjorden. Depths are given in meters

zooplankton from each depth interval was concentrated using reverse filtration; 4 aliquots were taken, from which 3 parts were used for respiration measurements and microscopy. For respiration measurements, zooplankters of each of the 3 aliquots were placed in 300 ml bottles filled with filtered seawater. These bottles plus 3 controls (filtered seawater only) were incubated on a rotating wheel for 18 h at 5 °C in the dark. Oxygen concentration in 3 control bottles before the incubation and in all other bottles after the incubation was titrimetrically measured (Graßhoff 1976), and the oxygen consumption was calculated. This procedure resulted in decreases in oxygen concentration by about 20 % in bottles containing zooplankters. Respiration in terms of daily carbon consumption was estimated by using a respiratory quotient factor of 0.85 (e.g. Hargrave 1973, Hatcher 1991) and assuming a constant rate of respiration over 24 h. After incubation, animals were examined microscopically using a dissecting microscope. The fourth aliquot from each zooplankton haul was dried and combusted (500 °C for 24 h) to obtain values for ash-free dry weight (AFDW). Zooplanktonic POC was estimated to be 50 % AFDW.

Sediment was sampled using a box corer (sampling area 900 cm^2). Subsamples were taken with plexiglass tubes (10 cm inner diameter) and stored at *in situ* bottom water temperature (about 6 °C) for 2 to 3 h. To determine respiration rates, 3 undisturbed cores were sealed with the original overlying water and incubated between 14 and 16 h at 6.0 ± 0.1 °C. The initial and final oxygen concentrations of the overlying water, which was stirred with an internal rotor in the lid of each core, were determined titrimetrically (Graßhoff 1976). Respiration in terms of carbon was estimated as for mesozooplankton. The particulate organic content of sediments was estimated in triplicate in 6 to 8 discrete depth layers by drying subsamples from each depth layer at 60 °C for 24 h and subsequently combusting them at 510 °C for approximately 22 h. Carbon content was approximated to be 50 % of particulate organic substance. After extraction in methanol from 1 cm^3 of sediment, chlorophyll *a* and pheopigments were measured (Holm-Hansen et al. 1965) in triplicate in 6 to 8 discrete depth layers. The extraction procedure for this measurement involved intensive mixing with a vortex mixer for 30 s, followed by 30 min at 5 °C in the dark and lastly centrifugation for 10 min. After removal of the macrobenthos, adenosine triphosphate (ATP) – a measure for living biomass – was extracted (Pamatmat et al. 1981) and measured by the luciferine-luciferase method (Witzel 1979) for the same discrete sediment layers as for organic substance. Living carbon biomass was estimated using a conversion factor of 250:1 (Holm-Hansen & Paerl 1972) for POC:ATP.

To estimate depth-dependent surface area of the sediments in Ramfjorden, the area between selected depth contours was measured using a Zeus Image Analyser (Estep & MacIntyre 1989) from topographic sea charts presented in Soot-Ryun (1922). At the site of investigation Ramfjorden is characterized by a steeply sloping bottom topography from the shoreline to the middle of the fjord, where maximum depths are about 80 to 100 m. The portion of the map of Ramfjorden within the rectangular overlay on the chart of the investigation area (Fig. 1) corresponds to 3.56 km^2. Within this rectangle, the portion of Ramfjorden with a bottom depth between 0 and 25 m is 0.96 km^2 or 27 % of the region of investigation. The portion between 25 and 50 m echo depth is 0.57 km^2 or 16 %. Between 50 and 100 m depth this area is 0.87 km^2 or 24 %. Below 100 m bottom depth the area is 1.17 km^2 or 33 % of the fjord within the box.

RESULTS

Suspended particulate material

The concentration of total suspended particulate material – seston (Fig. 2A) – varied from ca 1.5 to 4.0 mg l^{-1} over all sampled depths during the investigation period. No depth-related or temporal trend was observed. Suspended POC (Fig. 2B) ranged from ca 70 to 270 µg l^{-1}; no pattern was observed with respect to depth or time and a peak for all depths was observed on 14 November. With values from ca 0.03 to 0.20 µg l^{-1}, concentrations of suspended chlorophyll *a* (Fig. 2C) generally decreased with time. Values for chlorophyll *a* increased slightly from 9 to 14 November; a distinct secondary peak was observed on 1 December. Values for pheopigments (Fig. 2D) ranged from about 0.2 to 0.9 µg l^{-1} and were several times higher than for chlorophyll. For all depths a peak in pheopigments was observed on 28 November. With values of about 8, C/N ratios (by atoms) for suspended material were low on 14 November. In contrast, on 28 November C/N ratios were between 13 and 25.

Sedimented particulate material and loss rates

Sedimentation of total particulate material (Fig. 3A) ranged from ca 400 to 8000 mg m^{-2} d^{-1} over the investigation period and was generally highest at 70 m depth on any one date. Values increased in all 4 sampling depths over the first 3 collecting intervals from 9 to 21 November. From 21 November to 1 December sedimentation rates at 50 and 70 m were lower than during the first 3 intervals. Peak sedimentation rates in all depths were recorded during the last collecting interval from 1 to 5 December. Sedimentation

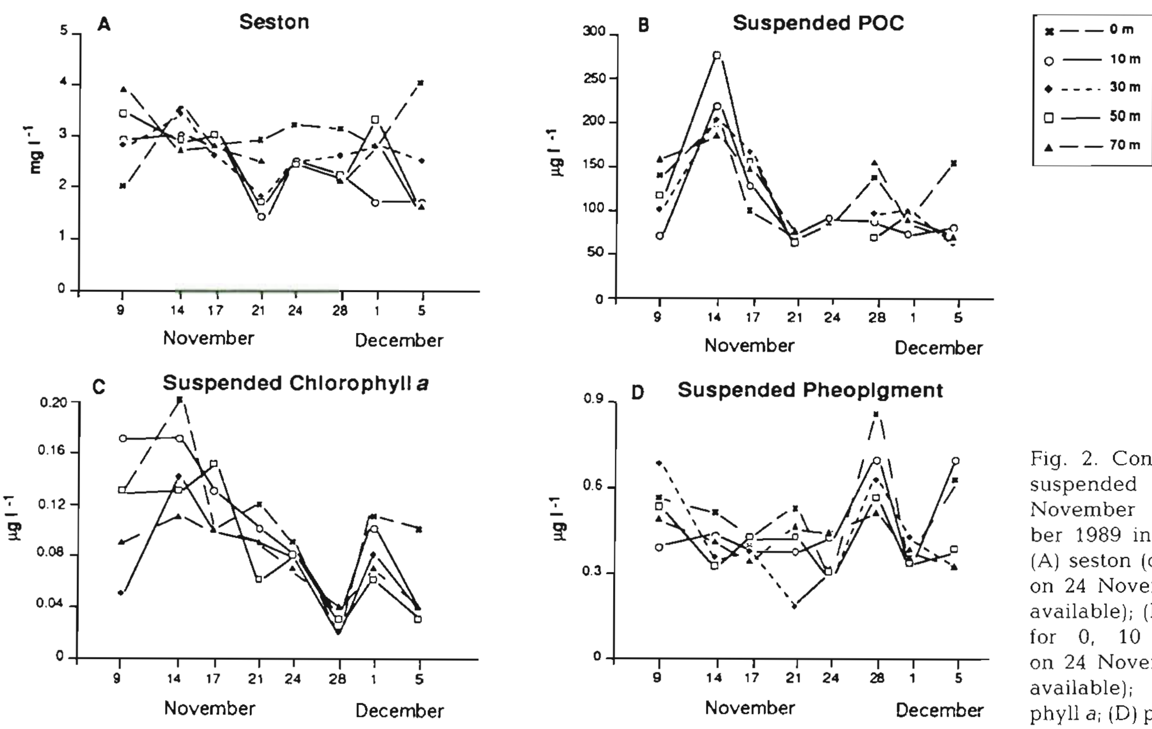

Fig. 2. Concentration of suspended material in November and December 1989 in Ramfjorden: (A) seston (data for 70 m on 24 November are not available); (B) POC (data for 0, 10 and 30 m on 24 November are not available); (C) chlorophyll *a*; (D) pheopigments

of POC (Fig. 3B) and chlorophyll *a* (Fig. 3C) ranged from ca 25 to 300 mg m^{-2} d^{-1} and 25 to 250 µg m^{-2} d^{-1}, respectively. The general temporal pattern of development for these 2 parameters was similar to that described for total particulate material. There were 2 exceptions. Firstly, sedimentation of POC at 70 m decreased over the first 3 sampling intervals and thereafter remained relatively constant until the period of 1 to 5 December. Secondly, sedimentation of chlorophyll *a* at 70 m remained almost constant over the first 5 intervals. Sedimentation rates for these 2 parameters increased with depth in almost all cases for any one collecting interval. Rates of sedimentation of pheopigments (Fig. 3D) ranged from less than 200 to about 2000 µg m^{-2} d^{-1}. For the upper 3 depths, the same pattern described for the other 3 parameters was observed, i.e. increasing rates from 9 to 21 November, lower relatively constant rates thereafter until 1 December and a surge in values during the last interval ending on 5 December. Sedimentation of pheopigments at 70 m, however, exhibited an absolute maximum rate of ca 2000 µg m^{-2} d^{-1} at the beginning of the investigation followed by a steady decrease until 28 November. As for all other biomass parameters a surge in sedimentation of pheopigments was observed at the end of the investigation. C/N ratios of sedimented material were generally between 9 and 12. Notably, the ratios ranged from 14 to over 15 during the sampling interval from 1 to 5 December.

Loss rates of POC due to sedimentation (Fig. 4) were highest in the upper 10 m of the water column and ranged from ca 1 to 14 % of suspended POC d^{-1}. Loss rates for the upper 30, 50 and 70 m ranged from ca 1 to 6 % d^{-1} with no depth-dependent pattern observed. Maximum values for all depth layers were recorded from 1 to 5 December. Down to depths of 10 and 30 m, secondary maxima were observed for the interval from 17 to 21 November. Small but distinct secondary maxima for the 50 and 70 m deep water columns were observed from 21 to 24 November.

Species composition of zooplankton

99 % of zooplankton collected was composed of small copepods. The dominant species were *Pseudocalanus acuspes* Giesbrecht, *Acartia longiremis* Lilljeborg, *Oithona* spp., *Microcalanus pusillus* G. O. Sars and *Microsetella norvegica* Boeck.

Carbon budget

A budget for the entire investigation period (Table 1) summarizes the mean size of the major carbon components of the Ramfjorden ecosystem as well as mean rates of respiration for the zooplankton and benthos. Temporal trends are not considered. Note that mesozooplanktonic POC is over 1 order of magnitude smaller than benthic biomass, even though benthic

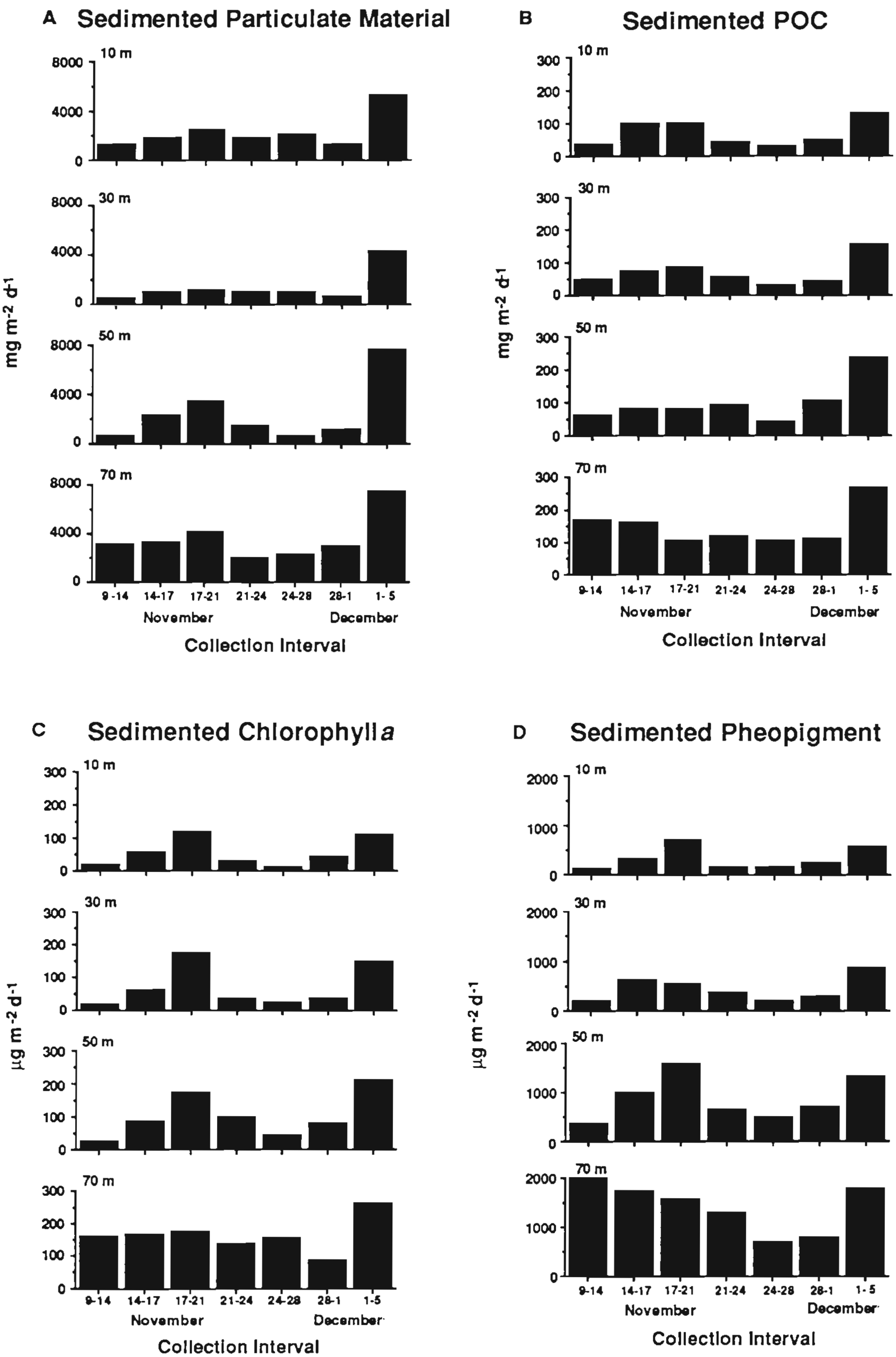

Fig. 3. Sedimentation rates in November and December 1989 in Ramfjorden: (A) particulate material; (B) POC; (C) chlorophyll *a*; (D) pheopigments

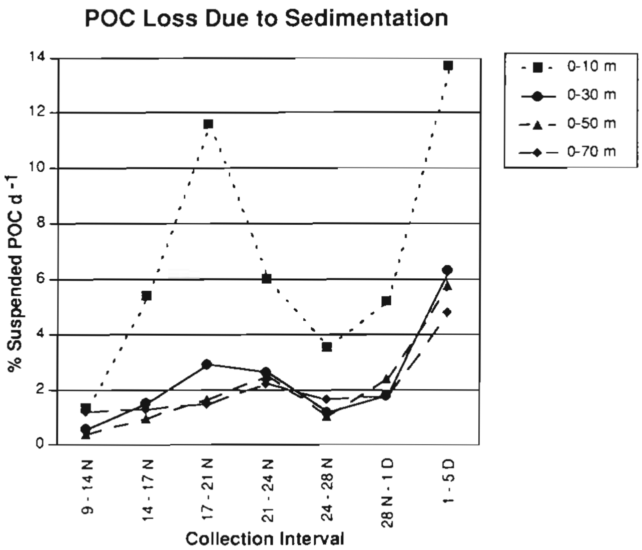

Fig. 4. Daily loss of POC due to sedimentation out of 4 depth layers. Loss rates refer to the amount of material sedimented out of the water column from the surface to the depth of respective sediment traps. For these calculations, values for suspended material were integrated over the respective range and the mean value for suspended material from 2 successive sampling dates was used as a basis for equating losses between these dates

macrofauna was not included in these estimates. Mesozooplanktonic respiration was small, i.e. never more than 0.14 % of suspended POC per day. Daily sedimentation at 30 m was equivalent to ca 2.4 % of suspended POC above 30 m for the entire investigation period. The corresponding rate measured at 70 m was estimated to be 1.9 %. Loss from the pool of suspended POC due to sedimentation at 70 m was about 25 times greater than that attributable to mesozooplanktonic respiration. Benthic respiration rates corresponded to approximately 0.35 % of suspended POC, were 36 and 18 % of sedimentation in 30 and 70 m, respectively, and were about 4.5 times greater than rates of mesozooplanktonic respiration.

DISCUSSION

Suspended and sedimenting material in the fjord in late fall/early winter

The light climate in this high-latitude system (Eilertsen et al. 1981, Eilertsen & Taasen 1984) changed rapidly in the 4 wk during which this investigation was conducted, with global radiation decreasing to an annual minimum by 17 November (data from the Norwegian Meteorological Institute, Oslo). This rapid change in environmental conditions was reflected in the concentrations of suspended chlorophyll *a*, which generally declined during the study (see also Eilertsen & Taasen 1984). However, short-term events were apparently related to advection, and pelagic structure at the onset and end of the investigation was charac-

Table 1. Flow of particulate organic carbon in Ramfjorden in early winter. Note that minimum and maximum ratios and percentages are calculated on a per sampling date basis. Values for mesozooplankton are for 0 to 70 m. Rates for benthic respiration are for micro-, meio-, and macrofauna; data on benthic biomass do not include macrofauna

	Suspended[a] ($mg\ C\ m^{-2}$)		Mesozooplankton ($mg\ C\ m^{-2}$)	Mesozooplankton respiration		Sedimentation			
				$mg\ C\ m^{-2}\ d^{-1}$	(% Susp.)[b]	$mg\ C\ m^{-2}\ d^{-1}$	(% Susp.)[b]	$mg\ C\ m^{-2}\ d^{-1}$	(% Susp.)[b]
	30 m	70 m	70 m			30 m		70 m	
Mean	3095	7818	265	6	(0.08)	74	(2.39)	151	(1.93)
Min.	1766	4537	145	3	(0.03)	33	(0.59)	106	(1.18)
Max.	6269	15644	547	14	(0.14)	160	(6.34)	273	(4.77)

	Sediment[c] ($mg\ C\ m^{-2}$)	Benthos[d] ($mg\ C\ m^{-2}$)	Benthic resp. $mg\ C\ m^{-2}\ d^{-1}$	Benthic resp. (% Susp.)[b]	Sedimentation/ Mesozoo. resp. 70 m	Benthic resp./ Mesozoo. resp.	Benthic resp. as % sedimentation 30 m	Benthic resp. as % sedimentation 70 m
Mean	178036	3438	27	(0.35)	25.2	4.50	36.49	17.88
Min.	154750	2175	14	(0.22)	11.7	2.42	17.92	10.47
Max.	197000	3900	38	(0.75)	62.5	9.61	72.03	31.23

[a] From the surface to given depth
[b] Percentage of carbon lost relative to suspended POC from the surface to given depth for sedimentation and from 0 to 70 m for respiration
[c] Sedimentary POC in upper 1 cm of sediment
[d] Living benthic biomass in upper 1 cm of sediment
[e] Percentage of carbon relative to sedimentation measured at given depths

terized by features significantly different from that during the middle of the investigation.

The first week of the investigation from 9 to 14 November showed increasing concentrations of suspended material which were moderate for this investigation and comparable with those from other studies in near-coastal waters (e.g. Noji et al. 1986). On 14 November peaks in surface POC and chlorophyll concentrations and a relatively low C/N ratio of about 8 were the distinguishing features of this phase. Presumably water containing raised levels of POC and chlorophyll *a* was advected from the more saline Balsfjorden into the investigation area, as indicated by increases in salinity of up to 0.17 ‰ below 10 m from 9 to 15 November at the investigation site. This may have been promoted by a rising tide at the time of sampling; the low and high-tide levels differed by ca 260 cm on 14 November. It was unlikely that phytoplankton growth at the investigation site caused the increases in POC and chlorophyll *a*, as primary production was presumably close to the annual minimum, i.e. near detection levels, in mid-November in Ramfjorden. Resuspension was also not a likely cause of the observed maxima for POC and chlorophyll *a* at the surface, as typical indicators, e.g. increases in C/N ratios, refractory material or detritus, were not observed. Although the taxonomic source of this chlorophyll *a* is not known, it was in the form of particles smaller than 15 µm in length, as the source was not evident from microscopy of objects ≥ 15 µm in length.

The distinct decrease in concentrations of suspended material immediately following the advective event was accompanied by a marked increase in sedimentation for all parameters, which indicated the low degree of recycling by pelagic processes, e.g. turnover by zooplankton (Noji 1991). Sedimentation rates were comparable with those often recorded in coastal waters (e.g. Smetacek 1980, Wassmann 1984, Noji et al. 1986), and values for sedimented POC were similar to those reported by Lutter et al. (1989) for the adjacent Balsfjorden for the month of February. In accordance with the diminishing pool of suspended particles and increasing sedimentation, the loss rate of suspended POC to sedimentation increased. This is particularly evident in data for the upper 10 m.

From 21 November to 5 December, the development of pelagic structure exhibited no consistent pattern, except for a tendency of diminishing chlorophyll *a* in all depths. However, 3 distinct features were exhibited. Firstly, a surge in suspended pheopigments and highest C/N ratios, i.e. between 13 and 25 by atoms, for suspended material in this investigation were recorded in all depths on 28 November. This was not accompanied by increased concentrations of chlorophyll *a*, which were at a minimum. As the pheopigment concentration of sediments was much higher than that of chlorophyll *a*, i.e. 4.89 ± 0.54 µg pheopigment cm^{-3} (n = 6) vs 0.79 ± 0.11 µg chlorophyll *a* cm^{-3} (n = 6) in surface sediments down to 2.5 cm, and since high C/N ratios are characteristic of many sediments (e.g. Smetacek 1980, Grebmeier et al. 1988), we conclude that resuspension and advection of sediments from adjacent shallow areas to the investigation site had occurred. Most likely, the event occurred shortly before hydrocast sampling on 28 November and the material was still in the process of settling, as the latter explains the higher concentrations of pheopigments in near-surface waters on this date. An increase in the sedimentation of pheopigments after 28 November was at least partly attributable to the resettling of this material.

The second unusual pelagic feature during this phase was a small but distinct secondary peak in chlorophyll *a* concentrations at all depths on 1 December. Although data on salinity are lacking for this date, the likely cause was the advection of a chlorophyll-*a*-richer body of water from the adjacent Balsfjorden to the investigation site. The incoming tide at the time of sampling may have played a role; high- and low-water levels in Ramfjorden differed by ca 190 cm on 1 December.

The third event was marked by an increase in suspended seston, POC and pheopigments in surface waters on 5 December. It is again concluded that resuspension and advection of shallow sediments caused these features. Sedimentation rates increased to peak or near-peak values for this study as did loss rates of POC to sedimentation. This was presumably a direct result of the settling of resuspended shallow sediments coupled with the sedimentation of the chlorophyll comprising the peak observed on 1 December. Further evidence of resuspension was provided by the large amount of detritus and sand grains as well as C/N ratios of about 14 to 15 (by atoms) for sedimented material, which were higher than for the previous 3 collection intervals.

Throughout the investigation sedimentation rates at 50 and 70 m were generally higher than at 10 and 30 m, whereby lowest rates for total particulate material and POC were at 30 m. This is typical of many shallow coastal marine system (e.g. Smetacek et al. 1978) and contrasts with the usual situation in open-ocean systems, in which surface-water productivity is often the chief source of sinking particles (e.g. Silver & Gowing 1991). The inverse situation in Ramfjorden in early winter supports the conclusion that a nonsurface-layer source of particles exists in the system. The generally larger amounts of detritus in the water column and sediment traps at 70 m relative to upper depths provide further evidence for the displacement of material from shallow to deep parts of the fjord.

Rates at 30 m appear to best represent loss of material from the surface layer. This conclusion is based upon the assumption that rates at 50 and 70 m were affected by resuspension, as indicated by the increased frequency of benthic fecal pellets in trap material at these depths, and that sedimentation rates at 10 m overestimate export since processes of recycling, e.g. grazing and remineralization, are still active below this depth. However, effects of resuspension were occasionally evident even at 30 m and above.

In addition, throughout the investigation loss rates for the upper 10 m were especially high, which reflected relatively high sedimentation rates and a relatively small measured POC load at the surface. This situation can result from the above described input of particulate material to the surface, which may occur in short-lived pulses recorded effectively by continuously collecting sediment traps but not through biweekly hydrocast sampling.

Sources and consumption of carbon

Assuming sedimentation rates recorded at 30 m are rates of export from the surface layer, it is estimated that the daily loss of pelagically produced POC due to vertical flux was ca 2.4 %. Further, zooplanktonic respiration could consume only a minor fraction (ca 0.1 %) of the suspended POC pool. Approximating a combined loss rate for POC (sedimentation plus respiration by mesozooplankton) from the surface layer to be 2.5 % d^{-1}, then a carbon source providing about 80 mg C m^{-2} d^{-1} must exist to maintain the load of suspended POC. Primary production at this time of year may be roughly 20 to 40 mg C m^{-2} d^{-1} as estimated from previous investigations in March by Bech (1982) and in November and February by H. C. Eilertsen (unpubl. data). Hence, much or most of the surface-water POC must originate from allochthonous sources such as runoff and resuspension of sediments.

Once sedimented, about 35 to 40 % of POC is aerobically consumed by the benthos. Thus in high-latitude systems where there is a continued input of food, benthic activity may account for a significant loss of POC from the ecosystem even in winter. Notably, benthic respiration was between 2 and 10 times greater than mesozooplanktonic respiration. This difference is probably due to the larger benthic biomass. In the upper 1 cm of sediment, living benthic carbon biomass (excluding macrofauna) was about 1 order of magnitude larger than mesozooplanktonic biomass in the entire water column on a per area basis. This indicates that specific mesozooplanktonic and benthic activities operate at similar levels at this time of year in Ramfjorden. The present findings suggest that an active benthic community several times larger than the community of mesozooplankton is sustained in early winter.

From the simple budget, it is evident that excess nonrespired POC can accumulate in deep parts of the fjord. The importance of this may be particularly evident in spring, when the input of freshly sedimented material may trigger intensified benthic consumption of older accumulated as well as new spring-produced organic matter (Graf et al. 1982, 1983, Graf 1987). Accumulation of organic matter in the deeper areas of fjords may be particularly intense, as the topography slopes rapidly from the shore to the middle of the fjord. In the region of investigation in Ramfjorden ca 65 % of sediments lie above a depth of 100 m. It may be expected that a considerable amount of macrophytic detritus as well as resuspended sediments are transported down the slope. Lateral advection of resuspended sediments is a phenomenon which has been modelled (Falconer & Owens 1990) and documented for other areas as well (e.g. Price & Skei 1975, Gilbert 1980, Lampitt 1985, Grant et al. 1987) including fjords (Lewis & Syvitski 1983, Domack & Williams 1990). In our investigation this presumably led to the redistribution of material to the deeper part of the fjord. Whether processes of flocculation are enhanced by the concentrating effect this process has on suspended material (e.g. Syvitski 1980) is not known. To what degree the dispersion of sediments influences bacterial respiration rates is also unclear, although it may be strong, as the resultant disruption of existing microenvironments and their associated biota (e.g. Sieburth 1991), increase in substrate area and possible oxygenation of anoxic or suboxic sediments may be significant.

CONCLUSION

In summary, the pelagic biological regime in Ramfjorden was senescing in November in response to the deteriorating light climate. This resulted in increasing sedimentation especially with respect to chlorophyll *a*. The pattern, however, was subject to perturbation by advection of pelagic material within the fjord and resuspension of sediments. Biological regulation of sedimentation, as can be induced by zooplankton via production and modification of feces (Bathmann et al. 1987, Lampitt et al. 1990, Noji et al. 1991, Voss 1991) and other processes (Banse 1990, Noji 1991), was not evident. Consumption of carbon was considerably greater by the benthos than by the mesozooplankton; this was probably due to the larger benthic biomass. The sedimentation of material, especially in the deeper parts of the fjord, was largely a result of the lateral advection of resuspended sediments and in terms of carbon was greater than the combined metabolic needs of the mesozooplankton and benthos. This process presumably leads to the accumulation of organic matter in the deeper parts of the fjord, which can be consumed during the spring period of intensified benthic activity.

This study was the first investigation to include data on plankton (e.g. Davis 1976, Falk-Petersen 1982, Hopkins et al. 1985, 1988, Bax & Eliassen 1990, Norrbin et al. 1990), sediments (Sargent et al. 1983) and sedimentation (Lutter et al. 1989) in Ramfjorden or in the adjacent Balsfjorden and one of the few to be conducted in a fjord in winter (e.g. Wassmann 1991). As such, although some reports on pelagic-benthic coupling in fjords exist (e.g. Hargrave & Taguchi 1978, Wassmann 1984, 1991, Skjoldal & Wassmann 1986), more research must be conducted to ascertain whether the presented findings are typical of fjord habitats in general and of Ramfjorden in particular. Nevertheless, the study may be an aid in understanding the flow of carbon in high-latitude regions and the importance of local hydrographic events in modifying pelagic structure.

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