

Use of chloroform in sediment traps: caution advised

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ABSTRACT: Experiments were conducted to study the effect of chloroform addition to sediment traps in the laboratory as well as in the field. Chloroform is an organic solvent which gave rise to extensive leaching of pigments and probably also other soluble organic compounds when fresh organic matter entered sediment traps. Droplets of chloroform suppressed microbial degradation of organic matter in the traps for a few days, but did not stop it. The presence of chloroform resulted in rapid anaesthesia of 'swimmers' such as cladocerans and copepods and their subsequent death. Thus, chloroform led to accumulation and disintegration rather than exclusion or preservation of 'swimmers'. The field and laboratory experiments suggested that loss of organic matter in unpoisoned traps was due more to 'swimmers' which entered, grazed and left the trap than to microbial degradation per se. Chloroform does not add significantly to the accuracy of vertical flux data. On the contrary, it gives rise to significant and undesirable side-effects, e.g. over- and underestimation of POC and chlorophyll *a* sedimentation rates, respectively.

INTRODUCTION

Sediment traps are the only tool available for directly measuring particle flux and composition in aquatic environments. However, we still need to improve the accuracy and precision of trap-derived flux estimates (GOFs 1989). When using sediment traps, 4 principle sources of error have to be considered: (1) hydrodynamic properties of the trap, (2) grazing and contamination by 'swimmers' inside the traps, (3) dissolution of inorganic matter and autolysis and (4) microbial degradation.

The hydrodynamics of sediment traps are relatively well known: the trap should have a cylindrical configuration, an aspect (height/diameter) ratio greater than 5, should be positioned vertically in the water, and not deployed in water where hydrodynamic energy is significant (Hargrave & Burns 1979, Bloesch & Burns 1980, Gardner 1980, Blomqvist & Kofoed 1981, Butman et al. 1986). However, even the appropriate configuration of sediment traps has been questioned again (GOFs 1989).

The remaining methodological problems mentioned above are still not adequately understood. The impact

of zooplankton and other animals which swim into the sediment traps ('swimmers') on estimates of the vertical flux has been known to be a potential source of error since the late 1970's (Smetacek et al. 1978, Fellows et al. 1981, Knauer et al. 1984) and has recently been evaluated in more detail (Harbison & Gilmer 1986, Lee et al. 1988). State-of-the-art estimates of vertical flux involve 'picking' (removal) of 'swimmers' prior to analysis (GOFs 1989). However, any method involving 'picking' of swimmers is based on an arbitrary operational definition based on the scientist's knowledge of zooplankton taxonomy, vertical migration of zooplankton and the participation of zooplankton in the vertical flux of organic matter. Only one method has been proposed so far which might *prevent* contamination by 'swimmers', namely the use of screens, a procedure which seems useful in specific areas where the size of settling particles is small (Karl & Knauer 1989). The exclusion of swimmers is for the time being the most prominent problem in obtaining accurate sedimentation rates.

Leaching, autolysis and microbial degradation of particulate and dissolved matter during trap exposure have also been subjects of discussion for some time (Bloesch & Burns 1980, Iseki et al. 1980, Gardner et al. 1983, Knauer et al. 1984). Preservatives (e.g. formaldehyde) and poisons (e.g. mercuric chloride, chloroform,

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sodium-azide) have been used inside traps to prevent or limit the impact of these processes. Preferably, chemicals that preserve the trap material rather than poisons that only kill organisms should be used during sedimentation studies. However, the effect of the additives on trap-derived vertical flux estimates has rarely been addressed. The ideal additive to a trap *preserves* the sedimenting material in the state of arrival inside the trap, *prohibits* microbial growth, *excludes* swimmers and introduces *no side-effects* during the chemical analysis. An additive with such qualities is presently unknown (GOFS 1989). Until recently, little attention has been paid to how effective certain poisons and preservatives are during trap exposure and what eventual side-effects they have on the quality and quantity of the material caught by traps (Bloesch & Burns 1980, Gardner et al. 1983, Knauer et al. 1984, Lee & Cronin 1984, Lee et al. 1988). The usefulness of additives to traps can be questioned not only because of their biasing effect on chemical analyses, but also because their decreasing effect on leakage, autolysis and microbial degradation is not exactly known and can be camouflaged by the bias introduced by the collection of swimmers which can disintegrate and mix with detrital material.

Chloroform, a poison commonly used by soil and sediment microbiologists (Novitsky 1986 and references therein), has been used in many sedimentation studies in the sea (Hendrikson 1975, Smetacek et al. 1978, Zeitzschel et al. 1978, Wefer et al. 1982, Lee & Cronin 1984, Peinert 1985). This is also the case for the majority of sedimentation studies from Norwegian waters (Wassmann 1983, 1985a, Skjoldal & Wassmann 1986, Ordemann 1987, Botnen 1988). Its high density and slow diffusion in seawater makes it very well suited as a poison in sediment traps. We investigated the effect of chloroform on the microbial degradation of different types of organic matter present in traps, using experiments conducted in the laboratory and in the field. Since we aimed to evaluate previous studies of vertical flux in coastal waters of Western Norway, the addition of chloroform and analysis of samples were the same as presented by Wassmann (1983). The effect of chloroform on the behavior of vertically migrating zooplankton was also studied.

MATERIAL AND METHODS

Three types of organic matter which are often found in traps deployed in the boreal, coastal zone were chosen for the laboratory experiments: 2 diatom cultures (*Thalassiosira bulbosa* and *Skeletonema costatum*) and detritus from the sediment surface. Diatom cultures were grown as a batch culture at 5 °C using the

nutrient medium IMR 1/2 (Eppley et al. 1967) and an irradiation of 70 $\mu\text{E m}^{-2} \text{s}^{-1}$. Addition of culture medium and air bubbling were stopped 3 d before the start of the experiments by removing the supernatant culture medium with a siphon, leaving the diatoms at the bottom. After suspending in fresh, unfiltered seawater, both cultures were stirred and separately siphoned into 2 series of five 1 l PVC beakers and stored at 10 °C in the dark. The final cell concentrations of the *T. bulbosa* and *S. costatum* used in the experiments were 1.6×10^8 and 2.9×10^8 cells ml^{-1} , respectively.

Benthic sediment was collected from the site of the field experiment (see below) by a SCUBA diver using a Ruttner water bottle after carefully resuspending the sediment surface. The sediment was screened (300 μm), siphoned into beakers and stored as described above. One series of the 3 types of organic matter was poisoned by adding 0.65 ml chloroform while the other was kept unpoisoned as a control. The experiment lasted for 15 d, and chemical analysis of subsamples from each beaker was performed every third day.

For the field experiments 3 moorings with cylindrical, duplicate sediment traps with a diameter of 10 cm (H/D-ratio of 5; distance between cylinders > 30 cm) and a vane, were deployed at 2 depths (Fig. 1) in the land-locked fjord Kviturdvikkollen (Dybern 1967, Wassmann 1985b). To one cylinder in each trap, 1 ml of concentrated chloroform was added with a pipette prior to deployment while the other was kept unpoisoned as a control. The polycarbonate collection

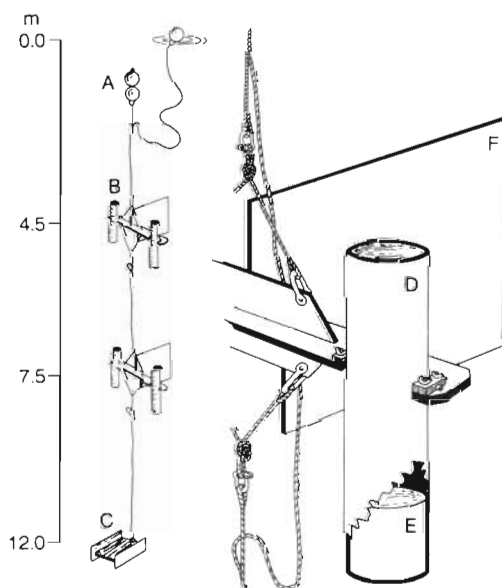


Fig. 1 Mooring system and sediment trap design used for the in situ experiment. A: subsurface buoy; B: duplicate sediment traps; C: anchor; D: cylindrical trap; E: polycarbonate beaker; F: vane

cups in the cylinders (Fig. 1E) are resistant to chloroform. The 3 moorings were simultaneously positioned within 10 m of each other and retrieved after 7 to 21 d. No sample replications were available. It is, therefore, assumed that each set of 3 double traps at the 2 depths collected the same amount of particulate material (Bloesch & Burns 1980).

The particulate material from the beakers and the sediment traps was continuously stirred for 30 min prior to sampling. Samples (20 ml) of the suspension were filtered in triplicate onto precombusted Whatman GF/C filters for analysis of particulate organic carbon and nitrogen (POC, PON), chlorophyll *a* and phaeopigments (Chl *a*, Phaeo) and stored frozen (-20°C) until analysis. Visible swimmers were removed from filters by forceps. The POC and PON samples were fumed with HCl to remove carbonates prior to analysis with a Carlo Erba strumentazione (1106) elemental analyzer. Chl *a* and Phaeo were analyzed fluorometrically after extraction in 90 % acetone according to Holm-Hansen et al. (1965) and Edler (1979). For bacterial enumeration formaldehyde (0.2 % final concentration) was added to a 20 ml suspension which was kept at 4°C until processing. Bacterial density was estimated by fluorescence microscopy using DAPI staining according to Porter & Feig (1980) for the *Thalassiosira bulbosa* and sediment samples.

In additional laboratory experiments, living zooplankton were added to beakers containing a *Thalassiosira bulbosa* culture (9.0×10^7 cells ml^{-1}). Only bacterial numbers as a function of time were recorded and the disintegration of zooplankton was visually examined. Moreover, the behavior of zooplankton was studied as a function of time in the presence of chloroform on petri dishes under a binocular microscope. The zooplankton (*Calanus finmarchicus* and *Evadne* sp.) were collected with a Juday net (160 μm mesh-size) by vertical hauls in the Raunefjord, close to the Department of Marine Biology, University of Bergen.

RESULTS

Laboratory experiments

The variations of POC and PON over time for the 3 types of organic matter are shown in Fig. 2. No clear trends indicating significant decomposition were found and even increasing concentrations were recorded. However, there was a tendency towards higher POC and PON concentrations in samples with chloroform addition. Filtration time of chloroform-treated samples increased with increasing time of the experiments, indicating higher retention efficiencies of the filters due to changes in the structure of the particulate mat-

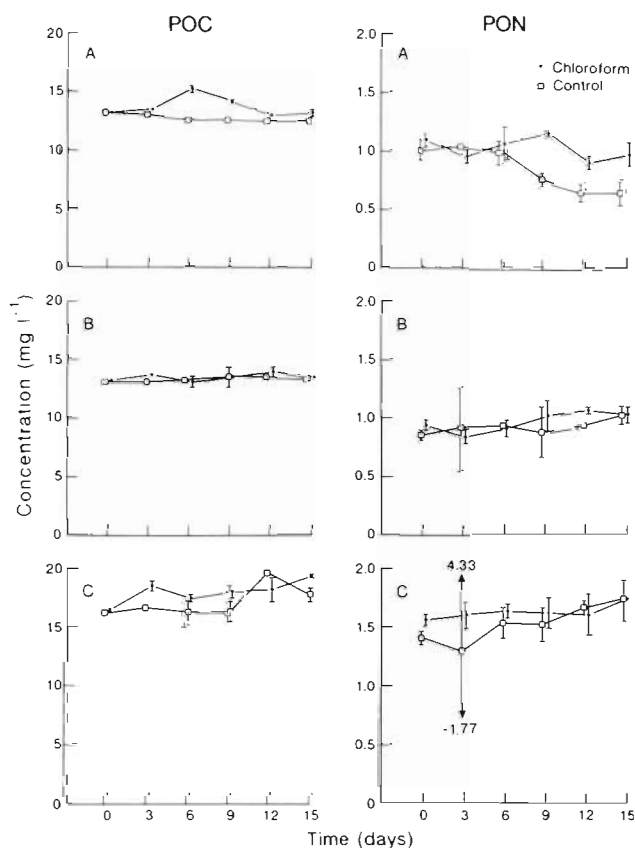


Fig. 2. Concentrations of particulate organic carbon and nitrogen (POC, PON) (mg l^{-1}) as a function of time for 3 types of organic material during an experiment with chloroform addition: (A) *Thalassiosira bulbosa*; (B) *Skeletonema costatum*; (C) benthic sediment. Vertical bars indicate 95 % confidence limits ($n = 3$)

ter. The question can be raised as to whether the choice of GF/C filters was reasonable, or whether GF/F filters should have been used. POC/PON ratios between 15 and 17 indicated strong nitrogen limitation in the algae suspensions at the start of the experiments (Table 1). Also the POC/Chl *a* ratios, especially those of *Skeletonema costatum*, indicate that the experiments were begun with algae in rather poor physiological condition (Table 1). The POC/PON ratios of *Thalassiosira bulbosa* and *S. costatum* decreased during the experiments and were slightly higher for the controls when compared to the chloroform-treated samples.

The concentration of Chl *a* in the *Thalassiosira bulbosa* and *Skeletonema costatum* series with the chloroform addition showed a significant decrease over time (Fig. 3). The control, however, showed unchanged or even increasing Chl *a* concentrations which might reflect Chl *a* production by shade-adapted phytoplankton in the dark. Chloroform is an organic solvent and the rapid decrease of Chl *a* during the first 3 to 6 d of the experiments indicates that the loss was most prob-

Table 1. Starting and average ratios of POC/PON (by atoms), POC/Chl *a* (by weight) and POC/dry weight (% by weight) of the organic matter in the laboratory (n = 6) and field experiments (n = 8). S: start; Cl: chloroform; C: Control

Type of material	POC/PON			POC/Chl <i>a</i>			POC/dry wt (%)		
	S	Cl	C	S	Cl	C	S	Cl	C
<i>Thalassiosira bulbosa</i>	15.1	15.7	18.6	127	316	132	37.5	36.4	34.6
<i>Skeletonema costatum</i>	17.3	16.1	16.9	420	1175	289	37.7	34.1	38.7
Sediment	12.8	12.6	13.1	2591	3620	3008	18.8	20.4	18.3
Field experiment									
4.5 m	–	9.7	9.3	–	3650	1221	–	23.2	18.3
7.5 m	–	9.9	9.7	–	2465	1096	–	19.9	19.0

ably caused by leakage of a loosely bound Chl *a* fraction of the diatoms. The Phaeo concentrations of the *T. bulbosa* series showed a decrease when chloroform was added, but the opposite was observed for *S. costatum* (Fig. 3). The composition of benthic sediment did not change significantly over time (Figs. 2 and 3). During the 2 phytoplankton sequences uptake of nitrate was recorded, apparently by bacteria (unpubl.)

Bacterial concentrations of the same magnitude were

found in both the poisoned and control sequences (Fig. 4). However, the increase in bacterial numbers was delayed for the poisoned sequences. This indicates that chloroform, when added at the beginning of the experiments, has a time-limited effect on bacterial growth, but is not an effective poison to decrease or even stop microbial degradation. The decrease of bacterial numbers was probably due to grazing of flagellates which together with ciliates were present in the beakers at concentrations up to about 1000 ind. ml⁻¹. Introduction of living zooplankton, which died after 3 and 6 d in chloroform-treated beakers and controls, respectively, resulted in bacterial responses comparable to those described above. The greatest bacterial numbers were recorded from beakers with zooplankton and chloroform additions (Fig. 4), indicating that the additional food source stimulated microbial degradation.

Field experiments

The sedimentation rates of POC and Chl *a* are shown in Figs. 5 and 6, respectively. Sediment traps with the chloroform addition always contained more POC than 'controls'. However, Chl *a* showed again the opposite trend (Fig. 6). The average ratios of POC and PON sedimentation rates derived from poisoned versus unpoisoned traps were 1.70 and 1.67, respectively; those for Chl *a* and Phaeo 0.68 and 0.99, respectively. A comparison of the sedimentation rates of POC and Chl *a* during consecutive time periods ranging from 7 to 21 d indicated that the rates from short periods ($\Sigma 7 + 7$, $\Sigma 7 + 11$ and $\Sigma 7 + 7 + 7$ d) were, in 20 out of 24 cases, higher than rates derived from longer exposure times (14, 18 and 21 d) (Table 2). This indicates that an increasing percentage of particulate organic matter is lost with increasing deployment time, even when chloroform is added. Particulate losses seem to be increasingly significant for deployment times greater than 10 d where loss rates of up to 60% were recorded (Fig. 7). Addition of chloroform to traps did not result in any pronounced difference compared to

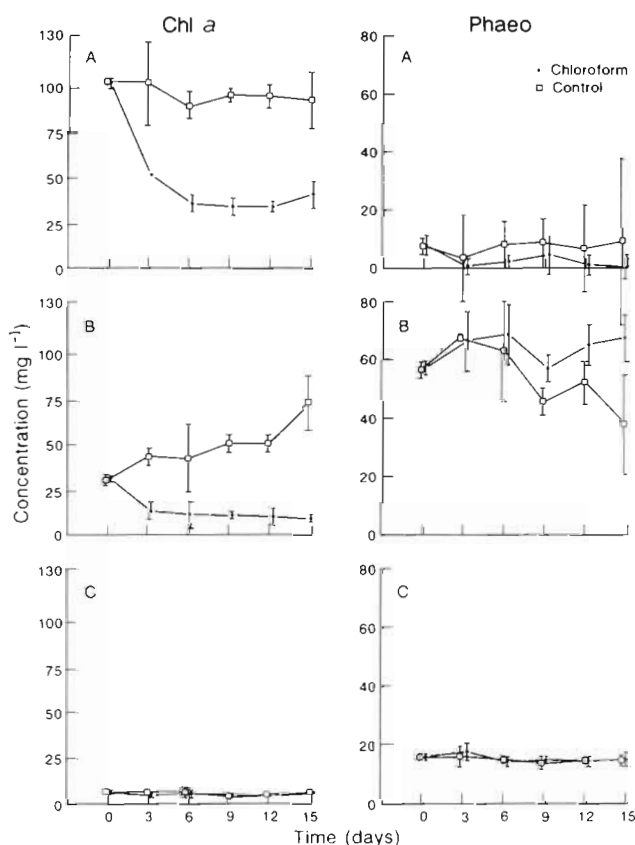


Fig. 3. Concentration of chlorophyll *a* and phaeopigments (Chl *a*, Phaeo) ($\mu\text{g l}^{-1}$) as a function of time for 3 types of organic material during an experiment with chloroform addition: (A) *Thalassiosira bulbosa*; (B) *Skeletonema costatum*; (C) benthic sediment. Vertical bars indicate 95% confidence limits (n = 3)

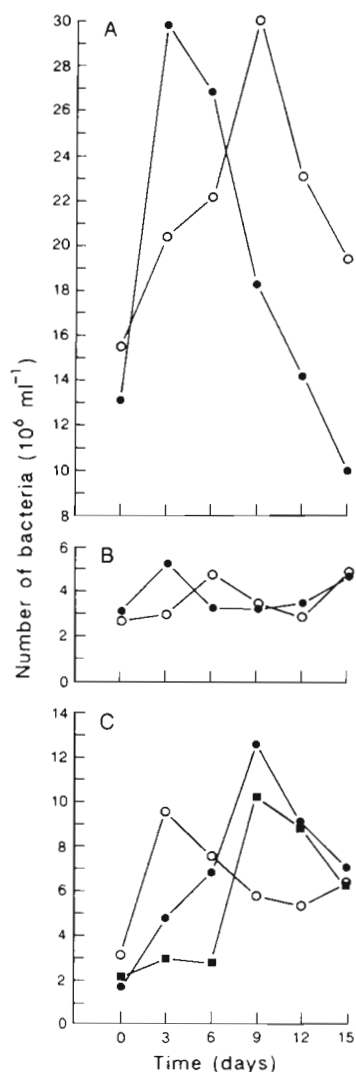


Fig. 4. Number of bacteria on particulate material as a function of time for 2 types of organic material during an experiment with chloroform addition: (A) *Thalassiosira bulbosa*, (B) benthic sediment, (○) chloroform; (●) control. (C) *T. bulbosa* with zooplankton addition, (●) chloroform + zooplankton; (○) zooplankton; (■) chloroform

controls over time, despite picking of visible swimmers (Table 2; Fig. 7).

Zooplankton behavior

After exposure to chloroform the swimming behavior of *Calanus finmarchicus* changed significantly during the first 2 to 3 min. The copepods started swimming on their sides or sank to the bottom upside down. Sudden, forceful swimming motions were observed. After 7 min all individuals lay on the bottom with small, sudden and cramp-like motions, becoming motionless after 10 min. When transferred to fresh seawater the copepods

started to move again after 10 min. After 20 min no further abnormal behavior was observed. This seems to indicate that copepods become quickly anesthetized when entering chloroform-treated traps. Therefore, once inside the chloroform-treated trap, copepods have no possibility of escaping and will die after about 10 min. In contrast, cladocerans (*Evadne* sp.) were quickly affected by and seemed to adhere to the chloroform droplets. After a few moments they were completely motionless. After transferring them to fresh seawater no sign of life was observed.

DISCUSSION

Bacterial numbers remaining within the same order of magnitude (Fig. 4) indicate that 1 ml concentrated chloroform did not suppress or stop microbial degradation in settling/suspended material during our laboratory experiments. Also in chloroform-treated sediment traps, substantial activity was found using ^3H -thymidine uptake as a measure of bacterial growth while this was negligible in formaldehyde-treated traps (Gundersen 1988). However, Lee et al. (1989) found complete cessation of bacterial activity on exposure to seawater with more than 50 % chloroform saturation. Gardner et al. (1989) found small differences in ash-free dry weight sedimentation rates derived from traps treated with 6 times more chloroform than in the present study (25 ml chloroform to 318 cm²; sediment suspension dried at 60 °C for 3 d) and from non-preserved traps in Lake Michigan, USA. This seems to suggest that the concentration of chloroform added to traps is of crucial importance for eliminating microbial breakdown. The lower the concentration, the less effective is chloroform as a poison. On the other hand, the higher the concentration, the more leaching of dissolvable organic matter will take place. The dilemma of chloroform addition to sediment traps lies, thus, in finding the optimal concentration.

Chloroform droplets do not mix with water and, given an appropriate aspect ratio, not only vertical but also horizontal diffusion plays a certain role in sediment traps. Studies of the diffusion of stained chloroform (unpubl.) revealed that chloroform was present in the lower part of the beakers and traps for at least 3 wk. However, little is known about the actual concentration across the bottom layer of the traps. Accumulation of sedimented matter in traps may also limit the diffusion of chloroform, as indicated by brown, oxidized sediment close to the chloroform droplets and reduced, black sediment further away (R. Peinert pers. comm.). High sedimentation rates and long deployment times may, therefore, decrease the effect of droplets of chloroform on microbial degradation of organic matter.

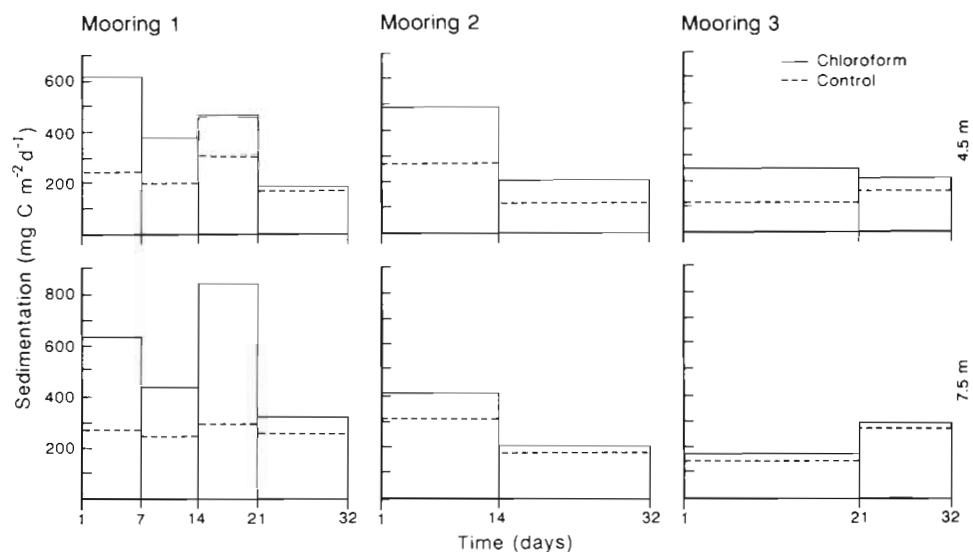


Fig. 5. Daily sedimentation of particulate organic carbon (POC) from 3 moorings at 2 depths during deployment time intervals ranging from 7 to 21 d ($\text{mg C m}^{-2} \text{d}^{-1}$)

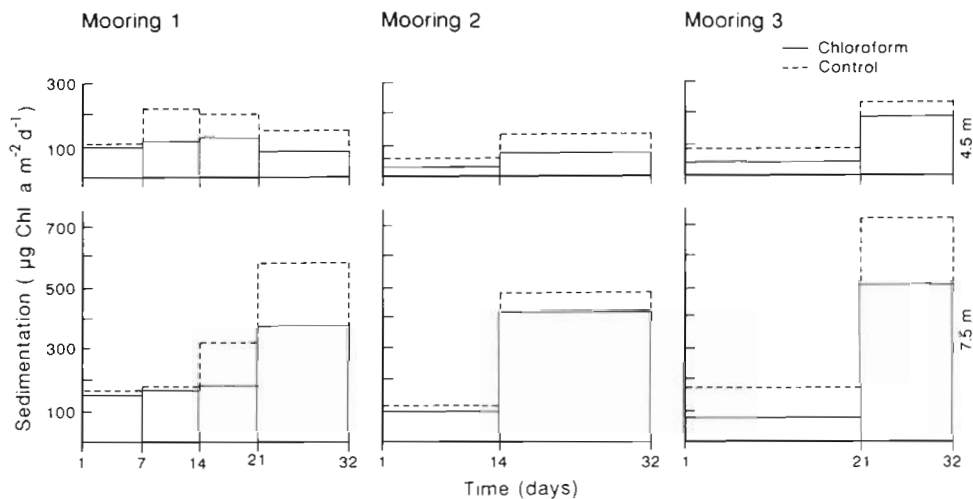


Fig. 6. Daily sedimentation rates of chlorophyll a from 3 moorings at 2 depths during deployment time intervals ranging from 7 to 21 d ($\mu\text{g Chl a m}^{-2} \text{d}^{-1}$)

Microbial food chains do develop in chloroform-treated sediment traps (Fig. 4) and have an impact on the quality and quantity of biogenic material caught by traps (Iturriaga 1979, Ducklow et al. 1985, Bauernfeind 1985, Taylor et al. 1986). However, the microbial degradation of the organic matter used during our laboratory experiments was apparently not sufficient to significantly reduce suspended POC and PON concentrations (Fig. 2). POC concentrations (13 to 20 mg l^{-1}) in the laboratory experiments are reasonable and would have reflected sedimentation rates of 240 to $370 \text{ mg C m}^{-2} \text{d}^{-1}$ during a 1 wk deployment period. The insignificant microbial degradation might be due to the rather poor nutritional quality of the organic matter used during the experiments (Table 1).

POC degradation rates of more than 50 % over periods of about 2 wk for *Skeletonema costatum* cultures (which had far lower POC concentrations than those in our experiments, and were continuously stir-

red during the incubation period) were reported by Bauernfeind (1985), Fukami et al. (1985) and Plett (1989). Such high degradation rates were not observed in our investigation. Sediment traps in coastal areas, which are characterized by high POC concentration and calm hydrodynamic conditions at the bottom of the traps, seem to experience far lower microbial degradation rates than less rich and stirred suspensions in laboratory experiments. However, some microbial degradation and certainly autolysis and leakage will take place inside the traps, especially during longer exposure times. The solute phase of sediment traps is ignored in most studies during sample processing and the true passive downward flux of biogenic matter is probably underestimated (Karl & Knauer 1989).

Since chloroform is an organic solvent, extraction of organic matter, such as loosely bound lipids, fatty acids and pigments, can take place (Goltermann 1964, Sargent & Falk-Petersen 1981). This is clearly shown by

Table 2. Ratios of long-term (14, 18 and 21 d) vs short-term (7 and 11 d) sedimentation rates of POC and Chl *a* at 2 depths, with and without chloroform (see Figs. 5 and 6). Cl: chloroform; C: Control

Period (d/d)	Depth 4.5 m		Depth 7.5 m	
	Cl	C	Cl	C
POC				
$\frac{14}{\Sigma 7+7}$	0.98	1.19	0.72	1.21
$\frac{18}{\Sigma 7+11}$	0.63	0.48	0.36	0.65
$\frac{21}{\Sigma 7+7+7}$	0.51	0.47	0.27	0.52
Chl <i>a</i>				
$\frac{14}{\Sigma 7+7}$	0.27	0.35	0.66	0.68
$\frac{18}{\Sigma 7+11}$	0.73	0.75	1.51	1.05
$\frac{21}{\Sigma 7+7+7}$	0.33	0.48	0.50	0.78

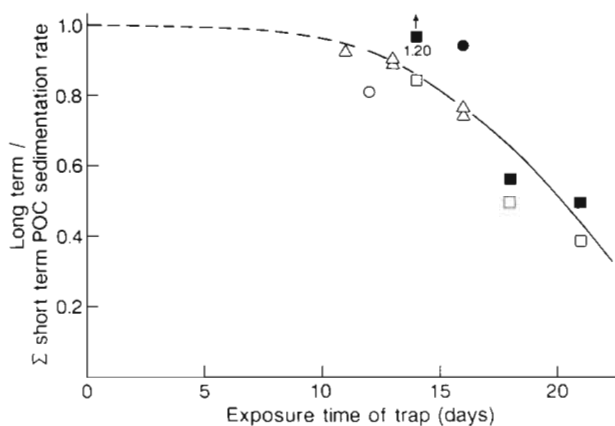


Fig. 7. Ratios of POC sedimentation rates derived from long term (11 to 21 d) versus Σ of short-term measurements (2 to 11 d) as a function of time. (○) Steele & Baird (1972); (●) Dörrstein (1977), cited by Bloesch & Burns (1980); (△) Bloesch & Burns (1980); (□), (■) this study (from Table 2): chloroform and control, respectively. Line is fitted by eye

the extensive leaching of Chl *a* in *Thalassiosira bulbosa* and *Skeletonema costatum* suspensions (Fig. 3). When studying the vertical flux of organic compounds which can be extracted by organic solvents such as chloroform, use of this additive is definitely not advisable. According to Hendrikson (1975) and Smetacek et al. (1978), chloroform tends to convert chlorophyll to phaeopigments, but prevents further breakdown that inevitably takes place if no preservative is added. Chloroform also increases phaeopigment concentrations when measured by fluorescence due to addition of pigment derivatives which do not belong to the

phaeopigments. The phaeopigment concentration in chloroform-treated samples should therefore increase with time. However, a reduction of Chl *a* and subsequent increase of Phaeo concentration was not found for chloroform-treated samples, neither in laboratory or in the field. The results of Hendrikson (1975) can thus not be supported by the present investigation. This might be partly due to leaching of pigments out of the particulate fraction during the experiments.

The mechanisms by which swimmers enter sediment traps are still not adequately understood. They may enter the traps by vertical migration, be attracted by the high food concentrations or become physically trapped when eddies enter through the trap opening. Poisons and preservatives cause the accumulation of swimmers; in the case of chloroform, due to anaesthesia followed by death. The breakdown of dead crustacean swimmers such as copepods is rapid (Honjo 1978), taking 3 to 11 d at temperatures between 4 and 10 °C (Harding 1975) and resulting in release of dissolved organic matter suitable for microbial breakdown.

Chloroform increased disintegration of zooplankton in both laboratory and field studies. Disintegration and decomposition make the removal of swimmers from trap samples difficult, but this is a necessary procedure in the estimation of an exact vertical flux rate (GOFs 1989, Karl & Knauer 1989). For example, Gardner et al. (1989) assumed the vertical flux estimates of lipids to represent the actual rates of supply to the benthos. However, about 25 % of the POC flux was due to lipids in chloroform-treated traps, while the non-preserved traps contained small amounts of lipids during summer. We suggest that part of the lipid flux measured by Gardner et al. (1989) was due to zooplankton contamination and that the presence and disintegration of swimmers were neglected in this study.

Zooplankton contamination may lead to an overestimation of organic matter such as POC and PON derived from chloroform-poisoned traps. In contrast, development of microbial communities inside unpoisoned traps, as well as the grazing and escape of larger swimmers during lengthy deployment times, may cause an underestimation of the vertical flux. For example, extensive losses of sedimented material from unpoisoned sediment traps in the euphotic zone of up to 43 % were recorded by Lee et al. (1987), most likely caused by zooplankton grazing and microbial degradation. The ratio of fluxes derived from poisoned versus unpoisoned traps is therefore greater than 1, as indicated by this and previous studies (e. g. Wassmann 1989). The substantial loss of POC and PON from the unpoisoned in situ traps and minor losses of POC and PON in the laboratory experiments without chloroform suggest that swimmers rather than microbial degradation are the cause.

Even during deployments of 1 wk neither the chloroform-treated traps nor the 'control' of the field experiment came close to the accurate sedimentation rate, which presumably lies between the 2 estimates. The limitations of chloroform use and the rapid loss of organic matter from sediment traps during deployments longer than 1 wk (Fig. 7) have consequences for all sedimentation measurements where chloroform has been used. Lengthy deployment times (e.g. Wassmann 1983, Wassmann 1985a) apparently give rise to underestimates of sedimentation of organic carbon. At specific, zooplankton-rich depth horizons, however, POC sedimentation rates greater than the integrated total primary production rate were recorded during summer (Wassmann 1985 a, b, Skjoldal & Wassmann 1986). This indicates the accumulation of organic matter due to disintegrated 'swimmers'. Organisms can, thus, both contribute and remove material from sediment traps and greatly change the calculated fluxes.

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LITERATURE CITED

- Bauernfeind, S. (1985). Degradation of phytoplankton detritus by bacteria: estimation of bacterial consumption and respiration in an oxygen chamber. *Mar. Ecol. Prog. Ser.* 21: 27–36
- Bloesch, J., Burns, N. M. (1980). A critical review of the sediment trap technique. *Schweiz. Z. Hydrol.* 42: 15–55
- Blomqvist, S., Kofoed, C. (1981). Sediment trapping – a subaqueous in situ experiment. *Limnol. Oceanogr.* 26: 585–590
- Botnen, H. (1988). Horizontale variasjoner i sedimenteringsraten av partikulært materiale i Spjeldnesosen, Lindåspollene. Master's thesis, Univ. of Bergen
- Butman, C. A., Grant, W. D., Stolzenbach, K. D. (1986). Predictions of sediment trap biases in turbulent flows: a theoretical analysis of based on observations from the literature. *J. mar. Res.* 44: 601–644
- Ducklow, H. W., Hill, S. M., Gardner, W. D. (1985). Bacterial growth and the decomposition of particulate organic carbon collected in sediment traps. *Cont. Shelf Res.* 4: 445–464
- Dybern, B. (1967). Topography and hydrography of Kviturdvikkollen and Vågsbøpollen on the West coast of Norway. *Sarsia* 30: 1–27
- Dörrstein, D. (1977). Sedimentation im Pilburger See (Orztal, Tirol). Ph.D. thesis, Univ. of Innsbruck
- Edler, L. (1979). Recommendations for marine biological studies in the Baltic Sea phytoplankton and chlorophyll. The Baltic Marine Biologists Working Group 9, 38 p.
- Eppley, R. W., Holmes, W., Strickland, J. D. H. (1967). Sinking rates of marine phytoplankton measured with a fluorometer. *J. mar. Res.* 1: 191–208
- Fellows, D. A., Karl, D. M., Knauer, G. A. (1981). Large particle fluxes and vertical transport of living carbon in the upper 1500 m of the northeast Pacific Ocean. *Deep Sea Res.* 28: 921–936
- Fukami, K., Simidu, U., Taga, N. (1985). Microbial decomposition of phyto- and zooplankton in seawater. I. Changes in organic matter. *Mar. Ecol. Prog. Ser.* 21: 1–5
- Gardner, W. D. (1980). Sediment trap dynamics and calibration: a laboratory evaluation. *J. mar. Res.* 38: 17–39
- Gardner, W. D., Hinga, K. R., Marra, J. (1983). Observation on the degradation of biogenic material in the deep ocean with implications on accuracy of sediment trap fluxes. *J. mar. Res.* 41: 195–214
- Gardner, W. S., Eadie, B. J., Chandler, J. F., Parrish, C. C., Malczyk, J. M. (1989). Mass flux and 'nutritional composition' of settling epilimnetic particles in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 46: 1118–1124
- GOFS (1989). Sediment trap technology. Report of the U. S. GOFS Working Group on Sediment Trap Technology and Sampling, US GOFS Planning and Coordination Office, Woods Hole
- Golterman, H. L. (1964). Mineralization of algae under sterile conditions or by bacterial breakdown. *Verh. int. Verein. Limnol.* 15: 544–548
- Gundersen, K. (1988). Degradation of organic matter in sediment traps. In: Wassmann, P., Heiskanen, A.-S. (eds.) *Sediment trap studies in the Nordic countries*, Vol. 1. Yliopistopaino, Helsinki, p. 22–37
- Harbison, G. R., Gilmer, R. W. (1986). Effect of animal behavior on sediment trap collections: implications for the calculation of aragonite fluxes. *Deep Sea Res.* 33: 1017–1024
- Harding, G. C. H. (1975). Decomposition of marine copepods. *Limnol. Oceanogr.* 18: 670–673
- Hargrave, B. T., Burns, N. M. (1979). Assessment of sediment trap collection efficiency. *Limnol. Oceanogr.* 24: 1124–1136
- Hendrikson, P. (1975). Auf- und Abbauprozesse partikulärer organischer Substanz anhand von Seston- und Sinkstoffanalysen. Ph.D. thesis, University of Kiel
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W., Strickland, J. D. H. (1965). Fluorometric determination of chlorophyll. *J. Cons. perm. int. Explor. Mer* 30: 3–15
- Honjo, S. (1978). Sedimentation of materials in the Sargasso Sea at a 5.367 m deep station. *Deep Sea Res.* 36: 469–492
- Iseki, K., Whitney, F., Wong, C. S. (1980). Biochemical changes of sedimented matter in sediment trap in shallow coastal waters. *Bull. Plankton Soc. Japan* 27: 27–36
- Iturriaga, R. (1979). Bacterial activity related to sedimenting particulate matter. *Mar. Biol.* 55: 157–169
- Knauer, G. A., Karl, D. M., Martin, J. H., Hunter, C. N. (1984). In situ effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. *J. mar. Res.* 42: 445–462
- Karl, D. M., Knauer, G. (1989). Swimmers: a recapitulation of the problem and a potential solution. *Oceanogr. Mag.* 2: 32–35
- Lee, C., Cronin, C. (1984). Particulate amino acids in the sea: Effects of primary productivity and biological decomposition. *J. mar. Res.* 42: 1075–1097
- Lee, C., McKenzie, J. A., Sturm, M. (1987). Carbon isotope fractionation and changes in the flux and composition of particulate matter resulting from biological activity during a sediment trap experiment in Lake Greifen, Switzerland. *Limnol. Oceanogr.* 32: 83–96
- Lee, C., Wakeham, S., Hedges, J. S. (1988). The measurement of oceanic particle flux – are 'swimmers' a problem? *Oceanogr. Mag.* 1: 34–36
- Lee, C., Wakeham, S., Hedges, J. S. (1989). Sediment-trap

- measurements of particle fluxes: effects of bacteria and zooplankton. In: GOFS. Sediment trap technology. Report of the U.S. GOFS Working Group on Sediment Trap Technology and Sampling, US GOFS Planning and Coordination Office, Woods Hole, p. 67–68
- Novitsky, J. A. (1986). Degradation of dead microbial biomass in a marine sediment. *Appl. environ. Microbiol.* 52: 504–509
- Ordemann, T. (1987). Sedimentering av partikulært materiale i Lindåspollene fra mai til oktober. Master's thesis, Univ. of Bergen
- Peinert, R. (1985). Saisonale und regionale Aspekte der Produktion und Sedimentation von Partikeln im Meer. Ber. Sonderforschungsbereich 313, Univ. of Kiel 2: 1–108
- Plett, R. J. (1989). Kinetics of microbial mineralization of organic carbon from detrital *Skeletonema costatum* cells. *Mar. Ecol. Prog. Ser.* 52: 123–128
- Porter, K. G., Feig, Y. S. (1980). The use of DAPI for identifying and counting aquatic micro flora. *Limnol. Oceanogr.* 25: 943–948
- Sargent, J. R., Falk-Pettersen, S. (1981). Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi*, and *T. inermis* during mid-winter. *Mar. Biol.* 62: 131–137
- Skjoldal, H. R., Wassmann, P. (1986). Sedimentation of organic matter and silicium during spring and summer in Lindåspollene, Western Norway. *Mar. Ecol. Prog. Ser.* 30: 49–63
- Smetacek, V., v. Bröckel, K., Zeitzschel, B., Zenk, W. (1978). Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographic regime. *Mar. Biol.* 47: 211–226
- Steele, J. H., Baird, I. E. (1972). Sedimentation of organic matter in a Scottish Sea Loch. *Memorie Inst. ital. Idrobiol. Suppl.* 6: 73–88
- Taylor, G. T., Karl, D. M., Pace, M. K. (1986). Impact of bacteria and zooflagellates on the composition of sinking particles: an *in situ* experiment. *Mar. Ecol. Prog. Ser.* 29: 141–155
- Wassmann, P. (1983). Sedimentation of organic and inorganic particulate material in Lindåspollene, a stratified, land-locked fjord in Western Norway. *Mar. Ecol. Prog. Ser.* 13: 237–248
- Wassmann, P. (1985a). Sedimentation of particulate organic material in Nordåsvannet, a hypertrophic, land-locked fjord in Western Norway. *Mar. Ecol. Prog. Ser.* 22: 259–271
- Wassmann, P. (1985b). Sedimentation of particulate material in two, shallow land-locked fjords in Western Norway. *Sarsia* 70: 317–331
- Wassmann, P. (1989). Sedimentation of organic matter and silicate from the euphotic zone of the Barents Sea. *Rapp. P.-v. Reün. Cons. int. Explor. Mer* 188: 108–114
- Wefer, G., Suess, W., Balzer, W., Liebezeit, G., Müller, C. A., Ungerer, W., Zenk, W. (1982). Fluxes of biogenic components from sediment deployments in circumpolar waters of the Drake Passage. *Nature, Lond.* 299: 145–147
- Zeitzschel, B., Diekmann, Uhlmann, L. (1978). A new multisample sediment trap. *Mar. Biol.* 45: 285–288

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