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Factors influencing organic carbon recycling and burial in Skagerrak sediments

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ABSTRACT

Different factors influencing recycling and burial rates of organic carbon (OC) were investigated in the continental margin sediments of the Skagerrak (NE North Sea). Two different areas, one in the southern and one in the northeastern part of the Skagerrak were visited shortly after a spring bloom (March 1999) and in late summer (August 2000). Results suggested that: (1) Organic carbon oxidation rates (C_{ox}) (2.2–18 mmol C m^{-2} d^{-1}) were generally larger than the O_2 uptake rates (1.9–25 mmol m^{-2} d^{-1}). Both rates were measured *in situ* using a benthic lander. A mean apparent respiration ratio (C_{ox}:O_{2corr}) of 1.3 ± 0.5 was found, indicating some long-term burial of reduced inorganic substances in these sediments. Measured O_2 fluxes increased linearly with increasing C_{ox} rates during the late summer cruise but not on the early spring cruise, indicating a temporal uncoupling of anaerobic mineralization and reoxidation of reduced substances. (2) Dissolved organic carbon (DOC) fluxes (0.2–1.0 mmol C m^{-2} d^{-1}) constituted 3–10% of the C_{ox} rates and were positively correlated with the latter, implying that net DOC production rates were proportional to the overall sediment OC remineralization rates. (3) Chlorophyll *a* (Chl-*a*) concentrations in the sediment were significantly higher in early spring compared to late summer. The measured C_{ox} rates, but not O_2 fluxes, showed a strong positive correlation with the Chl-*a* inventories in the top 3 cm of the sediment. (4) Although no relationship was found between the benthic fluxes and the macrofaunal biomass in the chambers, total *in situ* measured dissolved inorganic carbon (C_T) fluxes were 1–5.4 times higher than diffusive mediated C_T fluxes, indicating that macrofauna have a significant impact on benthic exchange rates of OC remineralization products in Skagerrak sediments. (5) OC burial fluxes were generally higher in northeastern Skagerrak than in the southern part. The same pattern was observed for burial efficiencies, with annual means of ~62% and ~43% for the two areas respectively. (6) On a basin-wide scale, there was a significant positive linear correlation between the burial efficiencies and sediment accumulation rates. (7) The calculated particulate organic carbon (POC) deposition, from benthic flux and burial measurements, was only 24–78% of the sediment

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trap measured POC deposition, indicating a strong near-bottom lateral transport and resuspension of POC. (8) A larger fraction of the laterally advected material of lower quality seemed to settle in the northeastern Skagerrak rather than in the southern Skagerrak. (9) Skagerrak sediments, especially in the northeastern part, act as an efficient net sink for organic carbon, even in a global continental margin context.

1. Introduction

The continental shelf and coastal zone cover less than 10% of the total ocean area but it accounts for more than 30% of the total primary production (PP) in the ocean (Berger *et al.,* 1989). Approximately 25–50% of this PP will settle on the sediment-water interface in these shelf areas (Wollast, 1991). A significant part of the particulate organic material (POM) reaching the sediment-water interface will be mineralized and recycled back to the overlying water column where it can further refertilize the euphotic zone with nutrients and thereby maintaining an often high primary productivity in coastal and shelf waters. The remaining POM in the sediment will be permanently buried and thus removed from the global carbon cycle for millions of years (Berner, 1980; Canfield, 1989). It is believed that 75–80% of all organic carbon undergoing long-term burial in the global ocean is actually buried in continental margin sediments (Liu *et al.,* 2000; Middelburg *et al.,* 1997). It is even suggested that this sedimentary sequestering of organic carbon is controlling the atmospheric oxygen level on geological time-scales (Berner, 1982; Berner and Canfield, 1989; Holland, 1984).

In some high accumulating continental margin seas, such as the Skagerrak (NE North Sea), up to 60–70% of the input of particulate organic carbon (POC) to sediments can get permanently buried (Hall *et al.,* unpublished results). Hence, in these areas preservation of organic material is of regional significance. Previous observations (e.g. Canfield, 1989, 1994; Henrichs and Reeburgh, 1987; Hulthe *et al.,* 1998) have shown that the fraction of deposited organic carbon (OC) that is buried tends to increase with increasing deposition rates to the sediments. However, recycling and burial rates of biogenic debris at the sediment-water interface do not only reflect the quantity but also the quality of the material reaching the sediment. The quality of settling particles is a key factor in understanding temporal variability in benthic metabolic rates. Several studies on both the continental shelf as well as in the deep-sea have shown a clear temporal variation in the sediment community oxygen consumption associated with episodic inputs of fresh phytodetritus (e.g. Boon and Duineveld, 1998; Pfannkuche, 1993; Smith *et al.,* 1992). Numerous studies have used chlorophyll *a* (Chl-*a*) and phaeopigments to characterize the quality of POM in the sediment (e.g. Ståhl *et al.,* 2004a; Sun *et al.,* 1991; Sun *et al.,* 1994; Witbaard *et al.,* 2000). Phytopigments, constituting a minor fraction ($<1\%$) of the total carbon pool in the ocean, can serve as a tracer for other highly labile material and biochemically important components (Boon and Duineveld, 1998; Gerino *et al.,* 1998).

Although it is well known that bacteria accounts for most of the mineralization of organic matter in marine sediments, several studies has shown that macrofauna can have a significant influence on the rates of these processes (Aller and Aller, 1998; Glud *et al.,* 1998; 2000). Irrigating macrofauna in the sediment can significantly enhance the oxygen

uptake rate by regularly ventilating their burrows with well oxygenated bottom water and thereby indirectly stimulating the bacterial community respiration (Forster and Graf, 1995; Vopel *et al.,* 2003). Several of the above mentioned processes and their impact on organic carbon remineralization have been investigated previously. However, most of these studies have dealt only with one of these processes at a time and few are based on *in situ* studies.

In this paper we present results from simultaneous measurements of different factors influencing organic carbon recycling and burial in the active and high accumulating margin sediments of the Skagerrak (NE North Sea). Both the quality and quantity of the incoming POC flux to the sea floor were investigated and coupled to lateral and vertical transport of POM. Using Chl-*a* as a tracer for highly labile organic matter in the sediment, the quality of the incoming POC was correlated with *in situ* benthic chamber measurements of organic carbon oxidation rates and oxygen fluxes. To investigate the spatial and temporal variation in these fluxes, measurements were performed in two geographically separated areas during two contrasting seasons, early spring (March 1999) and late summer (August 2000). An attempt was also made to directly determine the influence of macrofauna on these rates by correlating benthic *in situ* flux measurements with biomass of macrofauna collected from the benthic chambers. Finally, annual benthic mass balances of organic carbon are presented for the two different areas in the southern (H) and northeastern (K) Skagerrak.

2. Material and methods

a. Study site

The Skagerrak (Fig. 1) is a continental margin sea covering 32000 km^2 of both shelf and slope environments. It constitutes the deepest part of the North Sea with a mean depth of 210 m. The deep basin, called the Norwegian Trench (max depth 700 m), cuts through the entire Skagerrak in a northeastern to southwestern direction with a sill to the south at 270 m giving it a fjordic character (Fonselius, 1995). According to Fonselius (1995), the tidal currents are generally low (1–2 cm s^{-1}) with a tidal amplitude of 9–10 cm. The surface water exchange of the Skagerrak is dominated by a counter-clockwise circulation with water from the North Sea, with a salinity of 33–35 ppt, entering the southwestern Skagerrak via the Jutland Current. Low-saline (25–30 ppt) water from the Baltic Sea is transported with the Baltic Current northward through the Kattegat into the southeastern Skagerrak where it is mixed with the water from the Jutland Current. Water is exported out of the Skagerrak into the North Sea and the Norwegian Sea with the Norwegian Coastal Current along the Norwegian coast. The mean transport of water due to this cyclonic circulation is estimated at between 0.5 and 1.0 $\times$ 10^6 m^3 s^{-1} giving a flushing time above the sill depth of around 100 days (Rodhe, 1987). Surface temperatures ranged from 3 to 5°C between the different stations during the early spring cruise and from 15 to 16°C during the late summer cruise, whereas the bottom water temperature was rather constant at 6.6 to 7.4°C during both seasons (Table 1). Surface water salinities were the highest during the spring cruise, most likely due to wind driven mixing, and the lowest in summer due to the stratification of water masses (Table 1).

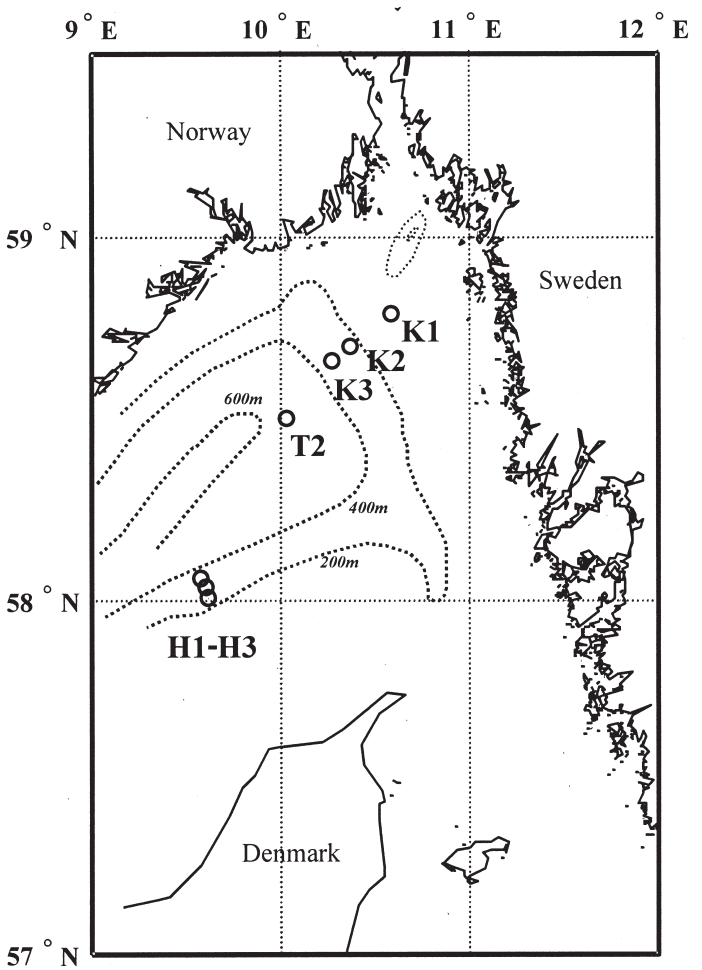

Figure 1. Map over the Skagerrak including the locations of the different sampling stations visited during the two cruises. Exact positions of the stations are given in Table 1.

Sedimentation rates have previously been found to be highest in the northeastern and eastern Skagerrak and least in the southern and deepest central part. Sedimentation rates, derived from ^{210}Pb profiles in the sediment, obtained in the vicinity of the K-area (northeastern Skagerrak) range from 0.22–1.0 cm yr^{-1} (Dennegård *et al.,* 1992; Meyenburg and Liebezeit, 1993; Van Weering *et al.,* 1987, 1993), whereas previous estimates close to the H- and T2 area (southern and central Skagerrak) range between 0.08–0.5 cm yr^{-1} (Anton *et al.,* 1993; Jørgensen *et al.,* 1990; Van Weering *et al.,* 1987, 1993; Hall *et al.,* unpublished results).

The shelf and slope sediments of the Skagerrak are highly variable and the extreme examples are the areas of erosion with sandy sediments along the Jutland Current (off the Danish north and northwest coast) and the very fine grained sediments in the Norwegian

Table 1. Dates, positions and hydrography data from all deployments made with the Göteborg benthic lander during the two expeditions in the Skagerrak. Sediment sampling with a multiple corer was made at the same stations. BW O_2: bottom water oxygen concentration/% saturation in bottom water. Bott. curr.: average bottom current speed using 1 minute sampling intervals during the entire deployment. Lat. transp.: calculated lateral SPM transport obtained from current speed and turbidity measurements ~2.5 m a b (±1 SD). Nm: not measured.

Station ID	Date	Pos. lat. N	Pos. long. E	W. depth (m)	Sal. (psu) surf./bott.	Temp. (°C) surf./bott.	BW O_2 (μM/ sat %)	Bott. curr (cm s^{-1})	Lat. transp. (g h^{-1} m^{-2})	Sediment type	Grain size (% sand/ % mud)
K1	Mar. 99	58°45.0′	10°37.3′	112	24.2/34.9	2.4/6.6	286/95	nm	nm	sandy mud	33/67
K2	Mar. 99	58°42.4′	10°21.9′	188	28.9/35.1	3.4/6.8	281/93	nm	nm	sandy mud	32/68
K3	Mar. 99	58°39.4′	10°15.6′	259	29.8/35.1	3.8/6.7	287/95	nm	nm	sandy mud	31/69
H2	Mar. 99	58°01.5′	9°35.8′	302	32.4/35.2	4.9/7.0	275/91	14.9	792 ± 132	sandy mud	33/67
H3	Mar. 99	58°02.2′	9°35.1′	356	33.7/35.2	5.8/7.0	277/92	17.6	2352 ± 1312	sandy mud	31/69
K2	Aug. 00	58°42.4′	10°21.9′	184	26.8/35.1	16.2/7.3	279/93	5.28	310 ± 134	sandy mud	32/68
K3	Aug. 00	58°39.4′	10°15.6′	259	31.6/35.3	15.3/7.2	266/88	6.92	342 ± 123	sandy mud	31/69
H1	Aug. 00	58°00.5′	9°36.9′	266	27.4/35.3	15.7/7.4	258/86	7.07	317 ± 116	muddy sand	65/35
H3	Aug. 00	58°02.2′	9°35.2′	350	28.4/35.3	16.1/7.1	263/87	8.87	353 ± 183	sandy mud	31/69
T2	Aug. 00	58°25.9′	10°03.0′	562	32.5/32.4	15.2/7.1	263/85	3.72	42 ± 27	sandy mud	31/69

Trench and parts of the eastern Skagerrak (Stevens *et al.,* 1996). The bottom water of the Skagerrak is well oxygenated with no observed seasonality in oxygen concentrations (Aure and Dahl, 1994). Benthic macrofaunal abundance typically varies between 1000 and 10 000 individuals m^{-2}, and the area contains a variety of different functional groups, i.e. passive filter feeders, notably ophiuroids (e.g. *Amphiura* sp.), surface deposit-feeding polychaetes and bivalves, and head-down feeding conveyor-belt-species (Josefson, 1981, 1985, 1986).

b. Benthic in situ flux measurements

Benthic solute fluxes of O_2 and total dissolved inorganic carbon (C_T) were measured *in situ* using the Göteborg benthic lander II, thoroughly described in Ståhl *et al.* (2004b), on seven different stations during two cruises in the Skagerrak (Table 1). The first cruise took place in early spring (March 1999) and the second in late summer (August 2000). The free-vehicle lander is equipped with four squared incubation chambers, each capable of closing off an area of 400 cm^2 of the sea floor. A "Mississippi-type" paddle wheel stirred the overlying water in the chambers during all incubations at a speed of approximately 60 RPM. For detailed information on hydrodynamic conditions in this and other chambers see Tengberg *et al.* (2004). The oxygen concentration in each chamber was measured at 1 min intervals with a Clarke-type oxygen electrode from Aanderaa Instruments (www.aanderaa.no). During the incubation, a series of 10 discrete water samples were withdrawn at pre-set times in 60 ml polypropylene syringes from each chamber. Bottom water samples, taken with a Niskin bottle mounted on the lander (2 m a b) and/or with CTD-Rosette casts (5 m a b), were used as the starting point of the incubation. Glass ampoules (20 ml), connected to three of the 60 ml sampling syringes on each chamber, were used to take samples for oxygen inside the chamber during the last cruise. These samples were used for calibration of the electrodes and as a backup for measuring the oxygen concentration change in the chamber. Each ampoule, originally filled with Milli-Q water, was flushed twice the volume with water from the chamber before the final sampling.

Each sample taken inside the chamber was replaced, through a diffusion barrier tube (1.5 mm i.d. and 400 mm long), by an equal volume of ambient bottom water from outside. Solute concentrations, measured in the bottom water outside the chamber, were used to compensate for the effect of this replacement water on the flux. This only resulted in a small (3–6%) correction of the measured flux depending on e.g. substance investigated, sample volume removed and height of the overlying water in the chamber.

Incubations lasted between 15–30 hours (typically ~20 h) and after termination of the benthic flux measurements the incubated sediment was brought to the sea surface together with the overlying bottom water in the chambers. This sediment recovery technique is similar to the one used on a multiple corer and gave the possibility to determine the precise water volume incubated in each chamber, which is essential for calculating the benthic flux. The lander was equipped with a Recording Current Meter model 9 (RCM-9) from Aanderaa Instruments for hydrographical recordings during the deployment. The RCM-9 was placed on top of the lander, ~2.5 m a b, above any possible disturbance. The RCM-9

allowed continuous measurements, at 1 min intervals, of pressure, conductivity, temperature, current speed, current direction, turbidity and oxygen concentration in the ambient bottom water (Table 1).

On the late summer cruise the lander was equipped with two sediment traps mounted directly on top of the lander with the mouth of the traps extending ~20 cm above the lander structure. The traps consisted of cylindrical, 55 cm long, polycarbonate tubes with an inner diameter of 8 cm, giving an aspect ratio of 6.9 which is within the range recommended to avoid selective trapping (Blomqvist and Håkanson, 1981). No poisons or conservatives were used in the traps. Before each deployment the traps were filled with a prechilled saltbrine (~70 g/L) to avoid mixing with ambient water. Immediately after collection the content of each trap was homogenized and three aliquots filtered through precombusted and preweighed Whatman GF/F glass microfibre filters (nominal pore size of 0.7 μm) for later determination of POC and PON.

It is well known that sediment traps not only collect vertically transported particulate material, but also can collect laterally advected material (Timothy and Pond, 1997; Walsh and Gardner, 1992). This can be due to resuspension of the sediment and in our case also to a small extent from resuspension created by the bow-wave of the lander itself upon landing. The top mounted turbidity sensor on the lander showed that at some stations (e.g. T2) the resuspended material caused by the landing reached the top of the lander. However, the amount of this lander-induced resuspended material was estimated to be negligible compared to the total amount of material collected by the traps.

To recover the lander it was fitted with a syntactic foam buoyancy package to make it ascend after the release of two ballast weights. After lander retrieval the water samples were treated in the following way: (1) Winkler reagents were immediately added to the O_2 glass ampoule samples and bottom water O_2 samples from the lander mounted Niskin bottle. (2) Samples for C_T, from the chamber syringes and Niskin bottle, were filtered through disposable 0.45-μm cellulose acetate filters prerinsed with 60 ml of ultrapure MQ-water. They were stored at *in situ* temperature for at most 24 h in clean 20 ml gas tight glass vials, with no headspace in the vial, before analysis on-board ship.

c. Flux calculations and corrections

Assuming a linear concentration change over time, the benthic flux (mmol m^{-2} d^{-1}) of O_2 and C_T in the chambers could be obtained. This was achieved by calculating the slope of the best-fit line, achieved by least square linear regression, of the concentration of a given substance versus time plot and multiplying this by the overlying water height in the chamber. Representative examples of the measured concentration change of O_2 and C_T versus time in the chambers are given in Figure 2. The uncertainty of the flux was calculated by estimating the error of the slope of the solute versus time data plots.

i. C_{ox} rate. In order to obtain the organic carbon oxidation rate (C_{ox}), the *in situ* measured C_T flux have to be corrected for any possible $CaCO_3$ dissolution taking place in the sediment (Anderson *et al.,* 1986; Berelson *et al.,* 1996; Hammond *et al.,* 1996; Ståhl *et al.,*

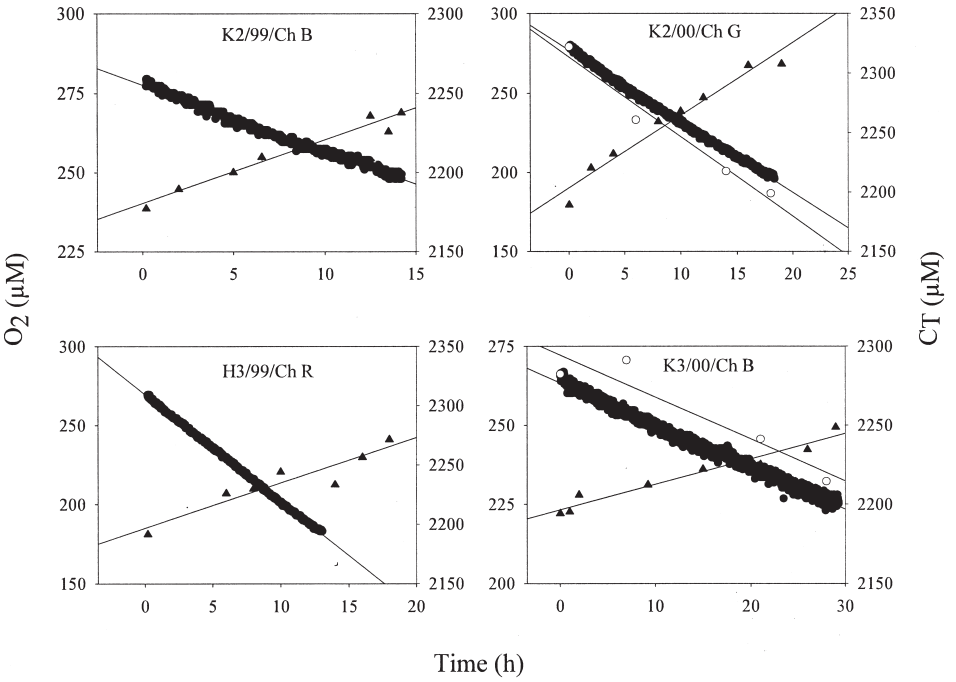

Figure 2. Representative examples of benthic flux incubations (stn/yr/chamber) made *in situ* with the Göteborg benthic lander. C_T (▲) was analyzed onboard ship (at ~20°C) in collected water samples from the lander. The O_2 concentration measured *in situ* with Clarke type O_2-electrodes (●) and by Winkler titrations (○). The regression lines used for calculating the benthic fluxes are indicated.

2004b). To investigate if and to what extent dissolution of $CaCO_3$ occurred in the study area, we collected solute flux samples for Ca^{2+} from the chambers followed by complexometric titration with EGTA and potentiometric detection (Lebel and Poisson, 1976). According to Lebel and Poisson (1976), the precision of this technique is 0.2‰ RSD which was by far exceeded in our measurements (3‰ RSD). Given the lower precision achieved in our measurements together with the high background concentration of calcium in seawater, a $CaCO_3$ dissolution of up to ~45% of the C_T flux could in the worst case take place in these sediments before we would be able to detect it. Therefore, a reliable estimate of the contribution from $CaCO_3$ dissolution to the C_T flux could not be obtained from our *in situ* Ca^{2+} flux measurements. The contribution from $CaCO_3$ dissolution to the C_T flux has previously been determined in several different continental margin and coastal sediments. For example, Berelson *et al.* (1996) calculated the dissolution rate to be 3–27% of the C_T flux in central California Borderland sediments (95–670 m depth). Green and Aller (1998) estimated the annual dissolution to be 20–50% of the C_T flux in Long Island Sound, whereas Silverberg *et al.* (2000) showed that 15–45% of the C_T fluxes were due to $CaCO_3$ dissolution in eastern Canadian continental margin sediments. In Aarhus Bay, which is a part of the Kattegat and thus closer to our site of investigation, Jørgensen (1996) found that

12% of the C_T flux was a result of $CaCO_3$ dissolution in the sediment. In laboratory incubations of sediment collected from several stations within the Skagerrak, Hulthe *et al.* (1998) estimated the $CaCO_3$ dissolution to be 7% of the C_T flux, and in the Gullmar Fjord, a nearshore area of the Skagerrak, Anderson *et al.* (1986) found this contribution to be even less (2%). Hence, there is a wide range of contributions of $CaCO_3$ dissolution to measured C_T fluxes in different types of sediments. This is probably depending on the type and amount of exoskeletons of planktonic organisms in the sediment as well as the saturation state of bottom water with respect to calcite and aragonite (Mucci *et al.,* 2000). Due to the lack of reliable data on $CaCO_3$ dissolution in this study, an average annual contribution from $CaCO_3$ dissolution to the C_T fluxes of 10% was estimated from the literature (Anderson *et al.,* 1986; Hulthe *et al.,* 1998; Jørgensen, 1996). This contribution was subtracted from the *in situ* measured C_T fluxes to obtain the C_{ox} rates.

ii. O_{2corr}. In order to discuss seasonal differences in the apparent respiration ratio (C_{ox}/O_2), the O_2 flux was corrected (O_{2corr}) for the contribution from nitrification to the O_2 flux assuming that for each mole of NO_3^- produced, 2 moles of O_2 was consumed. The nitrification rate was calculated as the sum of the NO_3^--efflux and the denitrification rate, obtained from pore water profiles of NO_3^- from each station (Brunnegård *et al.,* unpublished results). The NO_3^- efflux (J_{sed}) was calculated from the linear concentration gradient (dC/dz) between the nitrate maxima, usually within the top 5–10 mm of the sediment (Fig. 3), and the overlying water concentration using Fick's first law of diffusion ($J_{sed} = -\phi \cdot D_{sed} \cdot dC/dz$) (Berner, 1980). In the same way, the denitrification rate was calculated but from the linear portion of the NO_3^- profile below the nitrate maxima and 2–3 data points downwards (Fig. 3). The sediment molecular diffusion coefficient (D_{sed}) for NO_3^- was calculated by adjusting the D_{sw}, obtained from Schulz and Zabel (2000), to *in situ* temperature (~7°C) by the Stoke-Einstein relation (Li and Gregory, 1974) and correcting it for sediment tortuosity raised to the second power according to Boudreau's law (Boudreau, 1997) ($D_{sed} = D_{sw}/1 - \ln(\phi^2)$). The average D_{sed} for NO_3^- was $8.68 \cdot 10^{-6}$ cm^2s^{-1} at *in situ* temperature. Duplicate pore water profiles of NO_3^- were obtained from separate cores, generating two independent estimates of the nitrification rate at each station.

iii. DOC flux. Due to a rubber seal in the sampling syringes on the benthic lander the chamber-determined DOC fluxes were severely contaminated, often generating very high values (>200% of the C_{ox} flux). Therefore, sediment pore water gradients of DOC were instead used to model the sediment-water exchange of DOC. Since faunal activities such as bioirrigation and bioturbation play a major role in enhancing solute transport across the sediment-water interface in continental margin sediments (Aller, 1982; Aller and Aller, 1998; Forster and Graf, 1995; Glud *et al.,* 1994, 1998; Rutgers van der Loeff *et al.,* 1984; Vopel *et al.,* 2003), the DOC flux would most likely be underestimated if we solely applied the D_{sed} when modeling this flux with Fick's first law. Therefore, a biodiffusion/bioirrigation factor (α) was obtained as the ratio between the *in situ* measured C_T flux

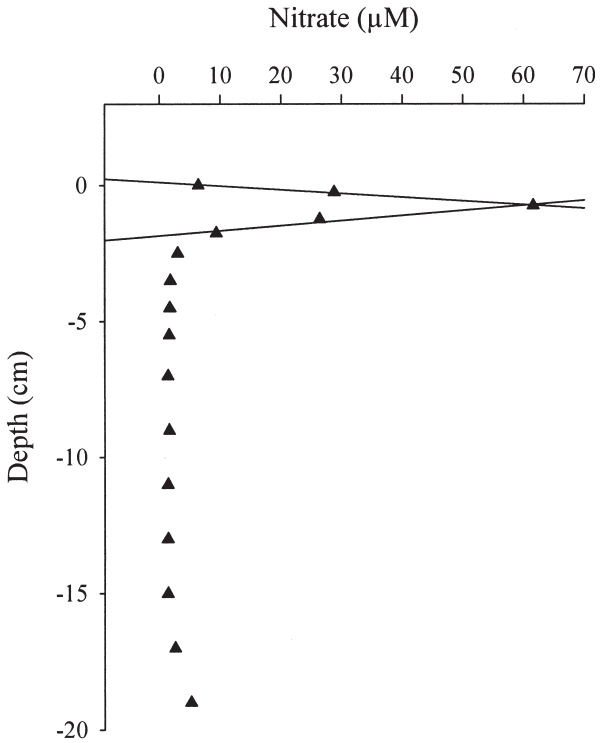

Figure 3. An example of a nitrate profile in the sediment. The regression lines indicate the concentration gradients used for calculation of the nitrate efflux (upper) and the denitrification rate (lower).

(J_{meas}) and the diffusive C_T flux (mean $D_{sed} = 8.16 \cdot 10^{-6}$ $cm^2 s^{-1}$ at *in situ* temperature). An apparent transport coefficient (D_{app}) could then be calculated by multiplying α with D_{sed} for DOC. By applying D_{app} to Fick's first law ($J_{DOC} = -\phi \cdot D_{app} \cdot dC/dz$), we obtained a DOC flux including the effect of biodiffusion and bioirrigation.

In conformity with C_T the steepest concentration gradients for DOC were always found in the top 5 mm of the sediment. The molecular weight of DOC was obtained from Burdige and Gardner (1998) who concluded, from ultrafiltration of different molecular size classes of DOC, that 60–70% of the pore water DOC in many continental margin sediments have molecular weights less than 3 kDa, and the remaining 30–40% were equally divided between the 3–100 kDa and >100 kDa fractions. Assuming that 65% of the pore water DOC in Skagerrak sediments was present in the 3 kDa fraction and 35% in the 100 kDa fraction, we obtained a mean D_{sw} of $1.02 \cdot 10^{-6}$ cm^{-2} s^{-1} at *in situ* temperature (Burdige *et al.,* 1992).

iv. Burial flux of organic carbon. Organic carbon degradation was assumed to be completed when the bulk sedOC (% dw) reached a stable asymptotic value at depth in the

sediment ($sedOC_\infty$), i.e. below the mixed zone at ~15–20 cm depth depending on the station and as indicated by the sedOC profiles. The organic carbon burial flux (OC_{burial}) could then be calculated by multiplying the $sedOC_\infty$ with the sediment accumulation rate (ω), obtained from sedimentary ^{210}Pb profiles from the same station.

d. Sediment sampling

Sediment cores, collected with a multiple corer (Barnett *et al.,* 1984), were used to obtain pore water distributions of C_T and DOC as well as solid phase distributions of inorganic- and organic carbon (sedIC and sedOC), porosity and radionuclides (^{210}Pb) from the same sites as the benthic lander was deployed. Cores (10 cm i.d.) with a seemingly undisturbed surface were immediately brought to a constant temperature room at close to *in situ* temperature (+6–7°C) for further processing on-board ship. Prior to slicing, the overlying bottom water in each core was sampled approximately 10 cm above the sediment surface and then carefully siphoned off. Cores were sectioned in 0.5 cm slices down to 2 cm depth, followed by 1 cm slices down to 6 cm depth and finally 2 cm slices down to 20 cm depth. The sediment was centrifuged at 2 100 rpm (~600G) for 30 min in clean polypropylene tubes. The supernatant was filtered through a Milli-Q rinsed 0.45 μm cellulose acetate filter. DOC samples were stored frozen at −20°C in acid and base cleaned polypropylene vials and C_T samples were analyzed onboard ship within a few hours after centrifugation. Subsamples for sedOC and sedIC were taken from the sediment solid phase after centrifugation. Whole sediment cores were stored frozen for later determination of radionuclide (^{210}Pb) distributions.

Chl-*a* sediment samples were taken during the 1999 spring cruise using an USNEL box corer, covering 0.25 m^2 of sediment. Three subcores were taken in each box core with plexi-glass tubes (4.5 cm i.d.) and when pressed into the sediment a piston was used to counteract compaction of the sediment inside the core. Each subcore was sliced into 1 cm horizons down to 20 cm depth in the sediment and from each slice a homogenized 1 ml sample was taken for Chl-*a* and immediately frozen (−20°C) and kept in the dark for at least 24 h. As for the 2000 summer cruise, Chl-*a* sampling was performed using a multiple corer instead of a box corer. Each of three subcores, taken by the multiple corer, was also sliced but with a somewhat coarser resolution at depth compared to the 1999 cruise.

For macrofauna, sampled in the incubation chambers of the lander, sediment was carefully sieved on deck through 0.5 and 1.0 mm mesh sieves with round holes. The sieve residues were fixed in 4% buffered formalin stained with Rose Bengal, sorted and later preserved in 70% ethanol. The biomass is given as formalin/ethanol wet weight after blotting on filter paper. Vermiform species were weighted (Mettler Toledo AG204) without tube structures and weights of molluscs included shells. In order to relate faunal biomass to respiration rates, wet weight measurements were converted into data for dry organic matter by using the conversion factors of Lie (1968). During the spring cruise, macrofaunal biomass and abundance were determined down to species level whereas on the summer cruise, macrofaunal biomass was determined down to the taxonomic groups of

Echinodermata, Mollusca, Crustacea, Polychaeta and Miscellaneous minor phyla (the latter including Cnidaria, Nematoda, Nemertea, Pogonopora, Sipuncula).

e. Analytical techniques

Determination of C_T in bottom water, flux chamber and pore water samples was performed on-board ship using an automated system based on non-dispersive infrared detection of CO_2 (Goyet and Snover, 1993; O'Sullivan and Millero, 1998). Prior to detection, all of the dissolved carbonate species in the samples were driven to CO_2 gas by acidification with phosphoric acid followed by nitrogen stripping. Running replicate measurements ($n = 10$) of certified reference material (CRM, Dickson Laboratories, Scripps Inst. of Oceanography, California), using a sample loop of 4 ml, an analytical precision of 0.2% RSD (SD $*$ 100/mean) was obtained. The instrument was furthermore calibrated and corrected for drift with this CRM. Winkler titration of dissolved oxygen concentration (Strickland and Parsons, 1972) was performed on bottom water and chamber samples with an analytical precision of 0.5% RSD ($n = 10$), using 10 ml samples.

DOC was determined using a SHIMADZU TOC-5000 total carbon analyzer based on the high-temperature catalytic oxidation (HTCO) technique (Sugimura and Suzuki, 1988). Samples were injected into a 680°C quartz combustion tube containing platinum on an alumina-support catalyst (3% Pt on Al_2O_3). Prior to the HTC oxidation of the DOC samples, inorganic carbon species were removed by adding 50 μl of high purity 2M HCl and purging the sample for 10 min with ultra pure air. All DOC samples were analyzed at minimum in triplicates with an analytical precision of 3% RSD ($n = 10$). The instrument was calibrated and corrected for drift with CRM:s distributed by Dr. D. Hansell, Bermuda Biological Station for Research, Inc.

Solid phase sediment samples for sedOC, sedIC and porosity were dried at 70°C for 24 h. Porosity was calculated from the weight of water loss from a known volume of wet sediment. After weighing, samples for sedOC and sedIC were ground into a homogenous powder with an agate mortar and pestle. For sedOC samples, careful removing of solid phase carbonates was obtained through repeated acid treatment (2M HCl) at room temperature until bubbling stopped (Hedges and Stern, 1984). Finally, combustion of the samples took place at high temperature (1050°C) using a Pisons Instrument model 1500CN CHN analyzer.

Cores taken for ^{210}Pb determinations were sliced in 3 mm sections for the upper 5 cm of the cores while the remaining part was sliced in 1 cm sections. Sediment accumulation rates were determined by the ^{210}Pb (half-life 22.4 yr) method. Roughly 0.5–2 g of dry sediment was digested in aqua regia and hydrofluoric acid in the presence of ^{209}Po acting as a yield monitor for the ^{210}Pb granddaughter ^{210}Po, which was used in the determination of ^{210}Pb. The polonium was deposited onto nickel-discs and determined by alpha spectrometry for about two days.

Samples for Chl-*a* were thawed and extracted in 96% ethanol for at least 6 hrs in the dark (Jespersen and Christoffersen, 1987). Volume of extraction fluid (10 ml) was 10 times the volume of the sediment sample to ensure complete extraction. Extracts were filtered

through a Whatman GF/F filter before analysis on a Turner model 10 fluorometer for Chl-*a* using the acid method (Strickland and Parsons, 1972). However, Chl-*a* is likely to be overestimated by this method (Falkowski and Sucher, 1981) and a more appropriate term would perhaps be the acid-labile fluorescent fraction at the actual wavelength. Nevertheless, for the sake of simplicity, we use the term Chl-*a* throughout the paper knowing that it may include other fluorescent substances.

f. Statistical analysis

The benthic lander was only deployed successfully at three (K2, K3 and H3) of the six main stations on both cruises. The other three stations were only visited once each, either on the spring or the summer cruise. This was due to technical malfunctions of the benthic lander, time limitations and disturbance from trawling activities in some of the investigated areas on the second cruise. The lack of sufficient replication of flux measurements within each cruise, as well as the uneven distribution of the performed measurements between the two cruises, hampered the use of a two-way Anova for statistical evaluation of the chamber flux data set. Simple t-tests (95% confidence interval), were performed to test for the effect of season and area on benthic fluxes (O_2, C_{ox} and DOC).

The data set for Chl-*a* concentrations in the sediment, from all stations during both seasons, were statistically evaluated using a two-factor Anova with replication ($n = 3$) with regard to the fixed factors of season (early spring vs. late summer) and area (K-stations vs. H-stations) as well as for any interactions between these two factors.

3. Results

a. Sediment characteristics and organic carbon burial

The sediment type at the different stations was mostly sandy mud approximately composed of 1/3 of sand and 2/3 of mud, except for Stn H1 which was muddy sand (Table 1). The deep central T2 station (562 m depth) had the most cohesive sediment with 31% sand and 69% mud, of which most was silt. The high percentage of sand at Stn H1 is most likely due to periods of high bottom stress at this location compared to the other stations. The central parts of Skagerrak experience weak bottom currents (Fonselius, 1995), thus having a higher percentage of small particles settling here (Canfield *et al.,* 1993a, b).

Porosity data support the grain size data with the lowest porosity at the sandier H1 station and the highest porosity at the T2 station with a high percentage of clay. The porosity ranged from 0.81 to 0.88 in the top 1 cm of the sediment between H1 and T2, and decreased with depth throughout the mixed zone below which it remained fairly constant at 0.68–0.78.

Bulk sedOC profiles (Fig. 4a) generally showed the same pattern at all stations with the highest values in the surface and decreasing with depth, except for station T2 which was more or less constant with depth. At the H-stations the surface sedOC content was 1.99–3.59 (% dw) and decreasing with depth to 0.96–1.76 (% dw) compared to the K1–K3 and T2 stations which had similar surface values of 2.52–3.54% dw, but higher values at

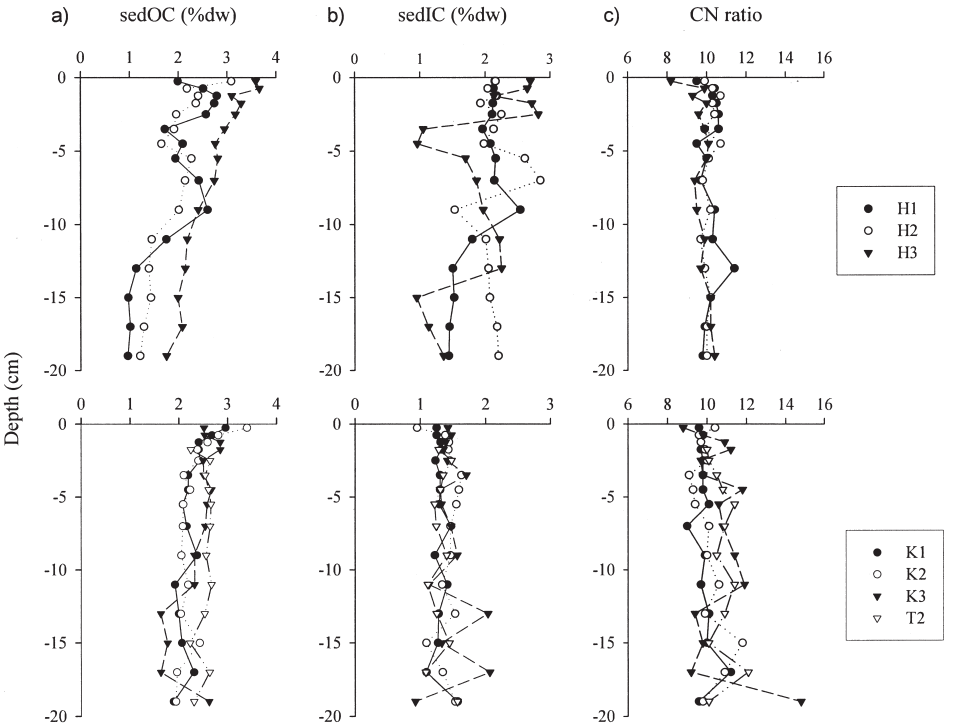

Figure 4. (a) Profile of sedimentary organic carbon (sedOC) at the H-area (upper) and K-area (lower). (b) Sedimentary inorganic carbon (sedIC). (c) C/N molar ratio in sediment.

depth (1.89–2.62% dw). Profiles of sedIC (Fig. 4b) remained rather constant around 1.3–1.5% dw from the surface down to 20 cm at the K- and T2 stations. At the H-stations the sedIC content of the sediment was considerably higher starting at 2.1–2.7% dw at the surface and slightly decreasing to 1.5–2.0% dw at depth. Sediment C:N molar ratios (Fig. 4c) were rather similar in the two areas starting between 8 and 10 in the surface layer and then slightly increased in the top 1 cm, possibly due to preferential nitrogen degradation. Most of the station C/N values stabilized at ~10 at depth although the deeper K3- and T2-station seemed to have somewhat higher C:N ratios at depth. However, they were difficult to interpret due to their scattery profiles.

Sediment accumulation rates ranged from 0.26–0.98 cm yr^{-1} in the K-area and from 0.26–0.71 cm yr^{-1} in the H-area. The lowest sedimentation rate (0.15 cm yr^{-1}) was found at the deep central T2 station. All cores (except T2) showed a close to homogenous ^{210}Pb distribution down to ~15–25 cm in the sediment, indicating a deep mixing on this timescale, followed by a linear decrease into the deeper layers (Fig. 5). The calculated OC burial fluxes ranged between 6.5–27.3 mmol C m^{-2} d^{-1}, with a total mean of 11.2 ± 7.6 mmol C m^{-2} d^{-1}. The northeastern K-area experienced higher OC burial rates (9.3–27.3 mmol C m^{-2} d^{-1}) compared to the southern H-area (6.0–8.9 mmol C m^{-2} d^{-1}). Although experiencing the lowest sediment accumulation rate the deep central T2 station

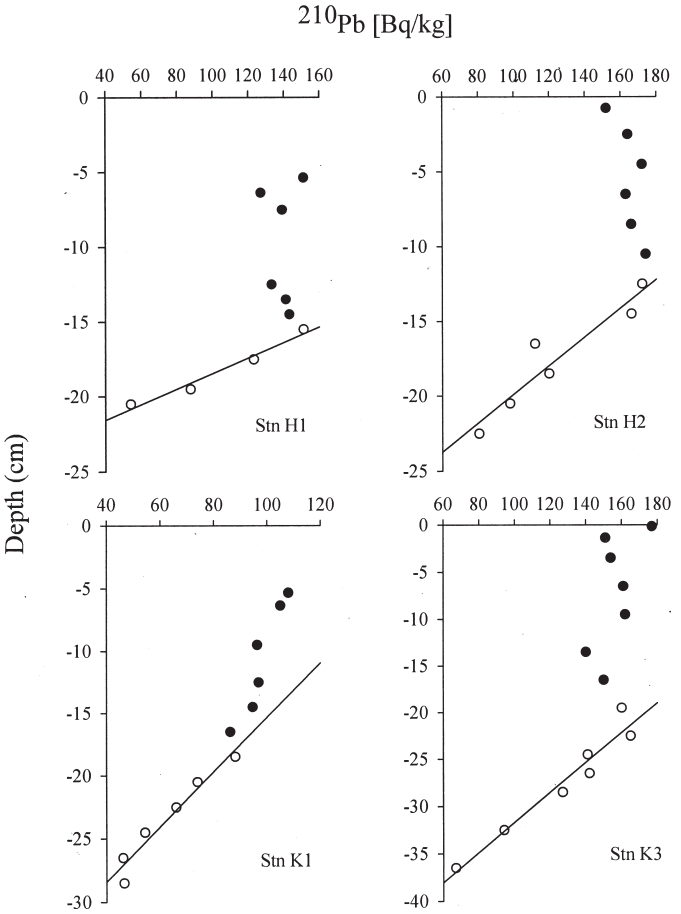

Figure 5. Profiles of unsupported ^{210}Pb at 4 stations. The surface mixed layer (●) was omitted in the linear regression. The regression lines used for calculating the sediment accumulation rates are indicated in the graphs (r^2 = 0.97 [H1], 0.90 [H2], 0.94 [K1], 0.94 [K3]).

had an OC burial flux of 6.5 mmol C m^{-2} d^{-1}, which is similar to or higher than some of the rates obtained at the H-stations.

b. Fluxes of O_2, C_T and DOC across the sediment-water interface

A total of 23 benthic O_2 and 22 C_T fluxes were measured *in situ* with the Göteborg lander during 10 deployments on six different stations during the two expeditions. Individual chamber O_2 fluxes on the two cruises varied between 1.89 ± 0.04–24.8 ± 0.02 mmol O_2 m^{-2} d^{-1} (± uncertainty of the individual flux), with a total mean of 7.74 ± 4.67 mmol O_2 m^{-2} d^{-1} (n = 23) (Table 2). The contribution from nitrification to the O_2 flux varied between the different stations from 2–13%, with a total mean of 7 ± 4% (n = 10). C_T fluxes varied between the individual measurements from 2.44 ± 0.92–20.0 ±

Table 2. *In situ* measured fluxes of O_2 and C_T from individual chambers at each station (± denote the uncertainty of the flux). O_{2corr} is the measured O_2 flux minus oxygen consumption during nitrification. C_{ox} rate is the C_T flux corrected for the mean contribution of $CaCO_3$ dissolution, estimated to be 10% of the C_T flux. Apparent respiration ratio is calculated by dividing the C_{ox} with O_{2corr}. Negative fluxes denote fluxes into the sediment.

Station/yr	Chamber ID	Incubation time (h)	O_2 (mmol m^{-2} d^{-1}) Flux	O_2 Uncert	O_{2corr} (mmol m^{-2} d^{-1}) Flux	O_{2corr} Uncert	C_T (mmol m^{-2} d^{-1}) Flux	C_T Uncert	C_{ox} rate (mmol m^{-2} d^{-1}) Flux	C_{ox} rate Uncert	C_{ox}/O_{2corr} (resp. ratio)
K1/99	—	—	*−8.40	—	−7.58	—	†14.0	—	12.6	—	1.66
K2/99	B	16	−5.33	*±0.02*	−4.61	*±0.02*	10.1	*±0.89*	9.12	*±0.8*	1.98
	G	16	−7.88	*±0.01*	−6.82	*±0.01*	20.0	*±1.22*	18.0	*±1.1*	2.64
K3/99	R	16	−5.77	*±0.07*	−5.49	*±0.07*	7.45	*±1.27*	6.71	*±1.1*	1.22
	B	16	−5.58	*±0.05*	−5.31	*±0.05*	6.96	*±0.56*	6.26	*±0.5*	1.18
	G	16	−2.04	*±0.03*	−1.94	*±0.03*	3.81	*±1.12*	3.43	*±1.0*	1.77
H2/99	R	20	−11.6	*±0.02*	−11.1	*±0.03*	8.06	*±0.76*	7.25	*±0.7*	0.65
	B	20	−9.73	*±0.04*	−9.31	*±0.04*	*13.5	—	12.1	—	1.30
	G	20	−7.57	*±0.02*	−7.24	*±0.02*	16.5	*±2.79*	14.8	*±2.5*	2.04
H3/99	R	20	−24.8	*±0.02*	−22.8	*±0.02*	13.9	*±2.33*	12.5	*±2.1*	0.55
	B	20	−1.89	*±0.04*	−1.74	*±0.04*	3.6	*±0.76*	3.24	*±0.7*	1.87
	G	20	−7.23	*±0.05*	−6.64	*±0.05*	11.4	*±3.77*	10.3	*±3.4*	1.55
K2/00	R	19	−5.02	*±0.02*	−4.51	*±0.02*	2.44	*±0.92*	2.20	*±0.8*	0.49
	B	19	−3.89	*±0.02*	−3.49	*±0.02*	6.51	*±0.94*	5.86	*±0.8*	1.68
	G	19	−13.9	*±0.02*	−12.5	*±0.02*	18.7	*±1.57*	16.9	*±1.4*	1.35
	W	19	−11.0	*±0.01*	−9.88	*±0.01*	15.7	*±1.00*	14.1	*±0.9*	1.43
K3/00	B	29	−5.75	*±0.01*	−5.17	*±0.01*	6.93	*±0.65*	6.24	*±0.6*	1.21
H1/00	R	29	‡−9.60	*±2.72*	−9.40	*±2.66*	9.63	*±1.09*	8.67	*±1.0*	0.92
	B	29	−6.72	*±0.02*	−6.58	*±0.02*	5.26	*±0.84*	4.73	*±0.8*	0.72
	G	29	−3.44	*±0.27*	−3.37	*±0.26*	4.02	*±1.00*	3.61	*±0.9*	1.07
	M	29	−8.16	*±0.03*	−7.99	*±0.03*	8.52	—	7.67	—	0.96
H3/00	R	19	−6.91	*±0.15*	−6.50	*±0.14*	8.47	*±1.73*	7.62	*±1.6*	1.17
	M	19	−8.85	*±0.02*	−8.32	*±0.02*	9.25	—	8.32	—	1.00
T2/00	B	25	−4.74	*±0.01*	−4.59	*±0.01*	5.52	*±0.75*	4.97	*±0.7*	1.08

*Calculated flux from the mean C_T/O_2 ratio within the K- or H-area, respectively.
†C_T flux calculated from pore water gradient with Fick's first law and taking into account the effect of biodiffusion/bioirrigation.
‡O_2 flux calculated from Winkler titrations of water samples taken in the chamber.

Table 3. Calculated diffusive (from gradient) and chamber-measured (*in situ*) C_T fluxes (±SD) used for calculating a biodiffusion/bioirrigation factor (α). DOC flux obtained by multiplying the diffusion coefficient for DOC with α.

Stn/yr	Diff. C_T flux (mmol m^{-2} d^{-1})	Meas. C_T flux (mmol m^{-2} d^{-1})	α	Calc. DOC flux (mmol m^{-2} d^{-1})	*DOC/C_{ox} (%)
K1/99	6.46 ± 0.87	14.0 ± 0.00	2.19 ± 0.30	0.88 ± 1.00	7.01 ± 1.13
K2/99	2.81 ± 0.31	15.1 ± 7.00	5.42 ± 0.60	0.83 ± 0.05	6.14 ± 0.47
K3/99	8.27 ± 1.73	5.83 ± 1.98	1.00 ± 0.00	0.18 ± 0.07	3.26 ± 0.50
H2/99	3.20 ± 0.70	12.7 ± 5.36	4.07 ± 0.89	0.97 ± 0.15	8.51 ± 0.37
H3/99	7.16 ± 5.07	9.62 ± 4.27	1.85 ± 1.20	0.84 ± 0.00	9.73 ± 0.56
K2/00	10.6 ± 5.53	10.8 ± 7.64	1.31 ± 0.44	0.46 ± 0.26	4.73 ± 0.90
K3/00	6.33 ± 2.81	6.93 ± 0.00	1.30 ± 0.42	0.49 ± 0.01	7.83 ± 0.01
H1/00	4.37 ± 1.37	6.86 ± 2.65	1.65 ± 0.51	0.15 ± 0.09	2.46 ± 0.73
H3/00	4.50 ± 1.14	8.47 ± 0.55	1.95 ± 0.49	0.46 ± 0.01	5.82 ± 0.07
T2/00	5.45 ± 0.01	5.52 ± 0.00	1.01 ± 0.00	0.24 ± 0.08	4.86 ± 0.34

*The DOC flux as percentage of the mean C_{ox} rate at each station.

1.22 mmol C m^{-2} d^{-1} (total mean 9.59 ± 4.90 mmol C m^{-2} d^{-1}, $n = 23$). Using all the available flux data for O_2 and C_T, from both H- and K-stations from each cruise, no statistical difference was detected either between early spring and late summer (O_2: $t = 0.29$, $P = 0.78$; C_{ox}: $t = 1.02$, $P = 0.32$) nor between the areas (O_2: $t = 1.06$, $P = 0.30$; C_{ox}: $t = 0.42$, $P = 0.68$).

The individual calculated DOC fluxes, including the effect of bioirrigation and biodiffusion, ranged from 0.13–1.59 mmol C m^{-2} d^{-1} at the various stations and with a total mean of 0.54 ± 0.39 mmol C m^{-2} d^{-1} ($n = 19$). Station mean values are presented in Table 3. No significant difference was detected between early spring and late summer fluxes, nor between the areas ($t = 2.19$, $P = 0.06$; $t = 0.38$, $P = 0.71$, respectively).

All the DOC profiles, used for calculation of the diffusive DOC fluxes across the sediment water interface, are shown in Figure 6. They typically increased twofold over the bottom water values (65–75 μM) in the top 0.5 cm of the sediment. For the K- and T2 stations the DOC concentrations continuously increased throughout the whole profile, never reaching a stable asymptotic value at depth. At station K1 and K3 the increase with depth was less (max 450–500 μM at 19 cm) than on the K2 and the deep T2 station (max ~1400 μM at 19 cm). At the H-stations the profiles showed more of a logarithmic increase with depth where the DOC concentrations stabilized at ~500 μM. The difference in the DOC profiles between stations in the H-area were less pronounced than in the K- (and T2) area. On stations where profiles from both seasons were obtained, the concentrations of DOC in the sediment were generally higher during summer than in spring.

Most of the pore water profiles of C_T (Fig. 7), used for calculating the biodiffusion/bioirrigation factor (α), display similar shapes as the DOC profiles although at a completely different concentration range. The α-factors varied from 1.01–5.84 with a total mean for all samples of 2.24 ± 1.48. Station mean values are presented in Table 3. A statistical difference in the biodiffusion/bioirrigation factor was found between the

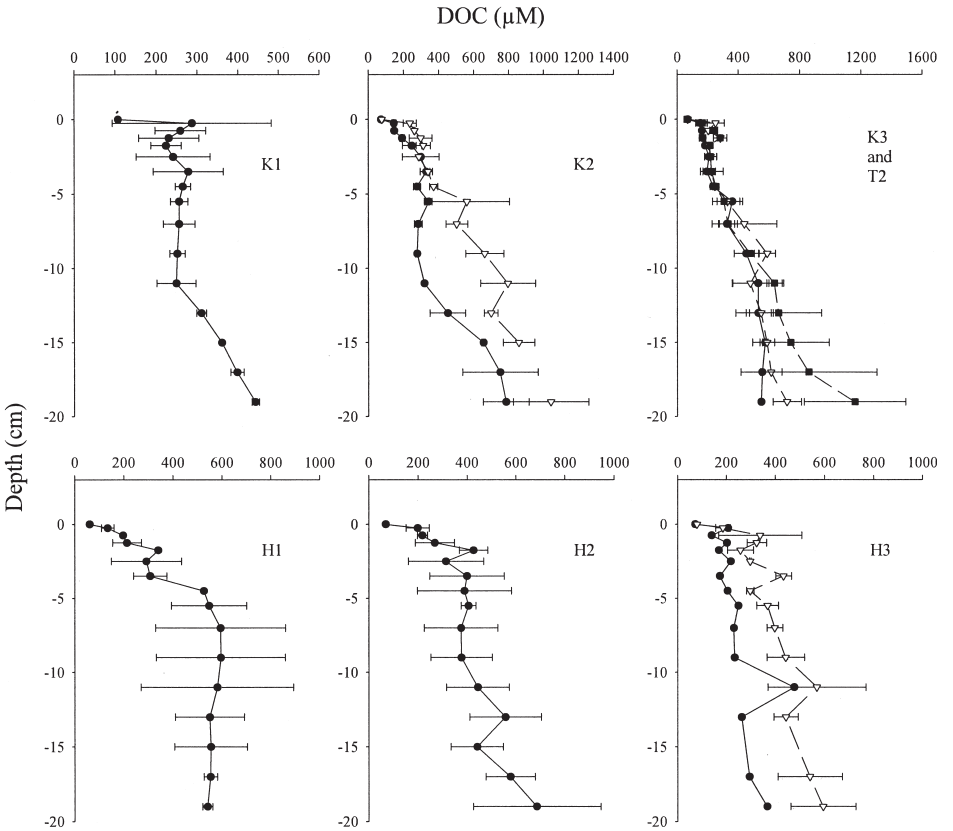

Figure 6. Average pore water profiles of DOC from spring (●) and late summer (△) at the different stations. T2 station (■), only visited during late summer, is plotted together with station K3. Error bars denote ±1 SD ($n = 2$).

seasons, with significantly higher α-values during the spring cruise compared to the late summer cruise ($t = 2.92$, $P = 0.01$).

c. Chl-a in the sediment

Concentrations of Chl-*a* in the sediment (Fig. 8) were in general higher on the early spring cruise compared to the late summer cruise, which corresponds well to the higher Chl-*a* concentrations measured in the euphotic zone in March 1999 compared to August 2000 (Maar *et al.,* 2002; Richardson *et al.,* 2003). This indicates that a phytoplankton spring bloom took place during and just prior to the early spring cruise. The Chl-*a* concentrations were always the highest just at the sediment surface and decreased with depth in the sediment except for station K3 in March 1999 where the concentration increased with depth, possibly due to nonlocal mixing. The greater variability within the spring profiles, especially in the upper part of the cores, compared to the summer profiles

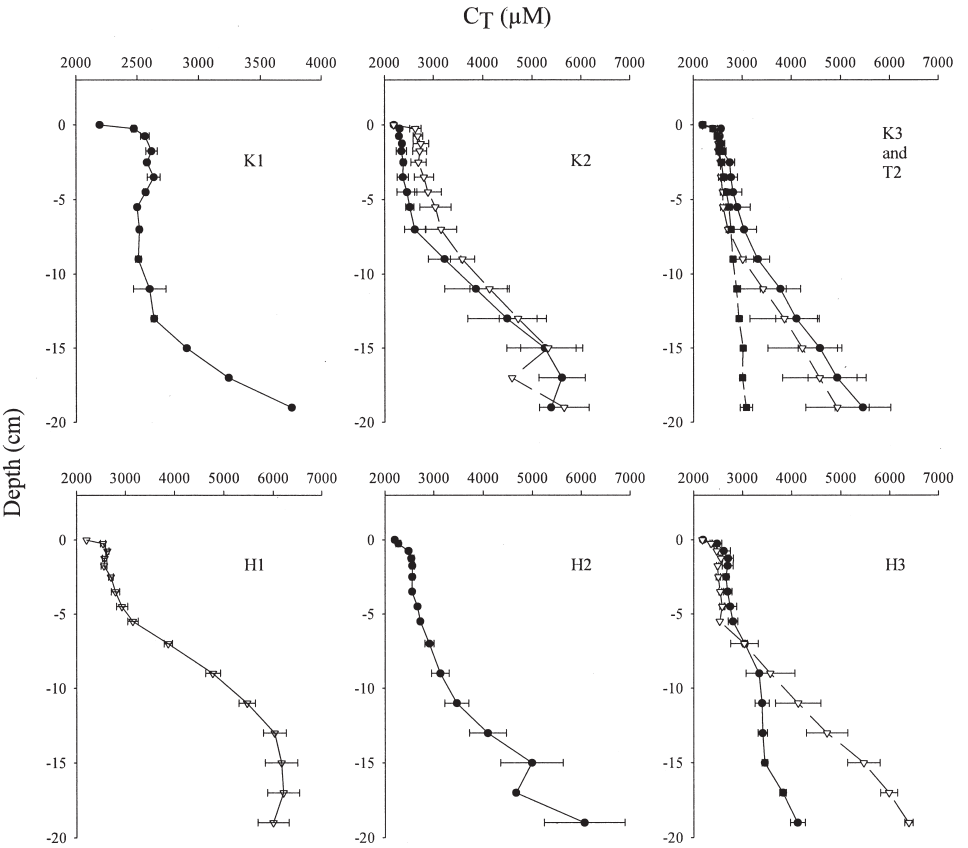

Figure 7. Average pore water profiles of C_T from spring (●) and late summer (△) at the different stations. T2 station (■), only visited during late summer, is plotted together with station K3. Error bars denote ±1 SD ($n = 2$).

indicated a more intensive mixing of the Chl-*a* in the sediment during March 1999 compared to August 2000. Surficial concentrations of Chl-*a* (mean value of 0–3 cm in the sediment) ranged between 1.01 ± 0.38–1.32 ± 0.51 μg Chl-*a* ml^{-1} ($n = 3$) at the H-stations and 0.60 ± 0.16–1.17 ± 0.28 μg Chl-*a* ml^{-1} at the K-stations during the spring cruise. On the summer cruise they ranged between 0.40 ± 0.10–0.73 ± 0.09 μg Chl-*a* ml^{-1} and 0.65 ± 0.10–0.77 ± 0.03 μg Chl-*a* ml^{-1} at the H- and K-stations, respectively. A statistically significant difference in the average Chl-*a* concentration (all stations) in the top 3 cm was found between the seasons ($F = 9.88$, $P = 0.01$ on the 95% confidence level), but not between the areas ($F = 0.07$, $P = 0.80$) or for any interaction between the two factors ($F = 1.29$, $P = 0.29$). However, single stations such as K3 in March 1999 and H1 in August 2000 were significantly different (single factor ANOVA, $P = 1.0 * 10^{-4}$ and $P = 3.1 \cdot 10^{-4}$, respectively, at the 95% level) from other stations in their respective areas. The difference in Chl-*a* concentration between the two seasons on

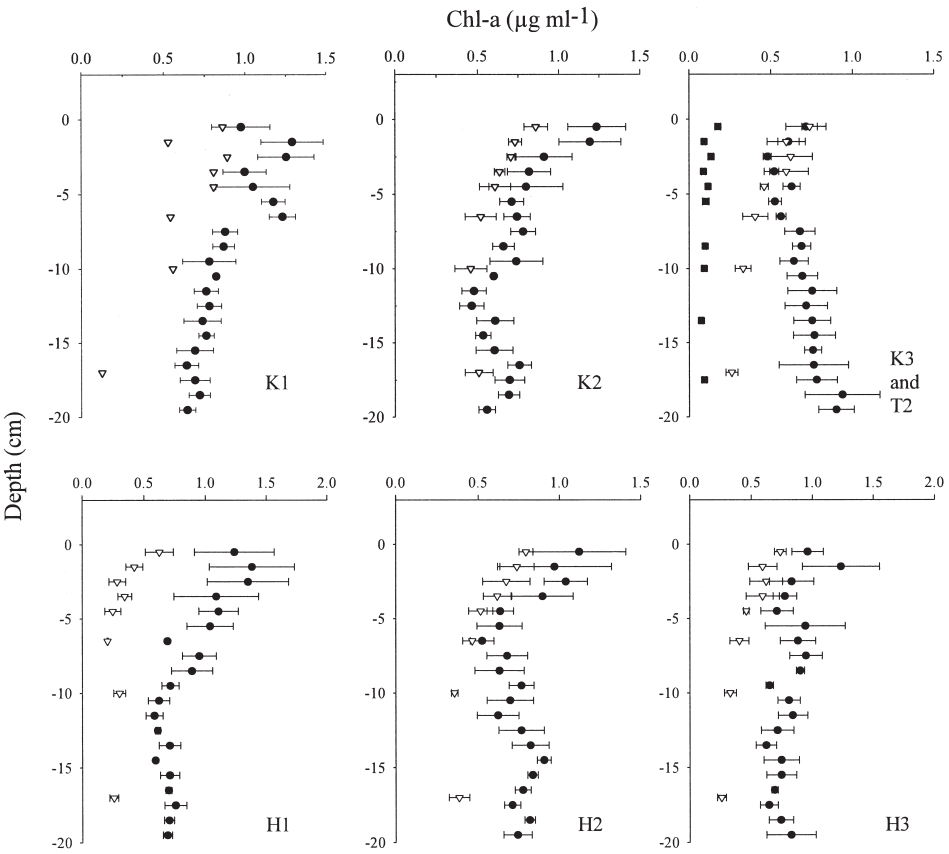

Figure 8. Average Chl-*a* depth distribution in the sediment from spring (●) and late summer (△) at the different stations. T2 station (■), only visited during late summer, is plotted together with station K3. Each profile is the mean of three multiple cores analyzed for Chl-*a*. Error bars denote ±1 SD ($n = 3$).

a single station was most pronounced at H1. Also the central T2 station, only sampled on the last cruise, had appreciably lower concentrations ($P = 5.67 \cdot 10^{-11}$) of Chl-*a* compared to both the H- and K-stations during the same cruise.

d. Sediment trap measurements and lateral sediment transport

The sediment trap collected total POC flux ranged from 14.3 ± 2.76 mmol C m^{-2} d^{-1} at the deep central T2 station to 63.0 ± 2.38 mmol C m^{-2} d^{-1} at the shallow H1 station (Table 4). The PON flux ranged from 1.53 ± 0.20–6.48 ± 0.43 mmol N m^{-2} d^{-1} on the same stations. Atomic C/N ratios in the traps were generally lower in the H-area compared to the K-area ranging from 8.99 at H3 to 10.9 at K2. Assuming that all of the Chl-*a* in the traps originated from primary production in the euphotic zone, the Chl-*a* flux were converted to estimates of phytoplankton carbon (Phyto-C) flux to the sea floor by using an

Table 4. Fluxes of particulate organic matter measured with the sediment traps mounted on top of the Göteborg benthic lander during the August 2000 cruise. (±SD).

Stn/yr	POC (mmol m^{-2} d^{-1})	PON (mmol m^{-2} d^{-1})	C/N (molar ratio)	*PhytoC (mmol m^{-2} d^{-1})	PhytoC/POC (ratio)
H1/00	63.0 (±2.38)	6.48 (±0.43)	9.72	2.89 (±0.22)	0.05
H3/00	57.1 (±4.08)	6.35 (±0.37)	8.99	2.84 (±0.41)	0.05
K2/00	47.8 (±3.70)	4.39 (±0.25)	10.9	1.68 (±0.50)	0.04
K3/00	39.3 (±9.66)	3.80 (±0.87)	10.3	1.17 (±0.24)	0.03
T2/00	14.3 (±2.76)	1.53 (±0.20)	9.33	0.49 (±0.06)	0.03

*PhytoC denote organic carbon originating from marine primary production calculated from the Chl-*a* in the traps, assuming a weight ratio for Phyto-C:Chl-*a* of 60 (Sun *et al.,* 1991).

average weight ratio Phyto-C/Chl-*a* of 60 according to Sun *et al.* (1991). The Phyto-C flux ranged from 0.49–2.89 mmol C m^{-2} d^{-1} between the T2 and the H1 stations. The Phyto-C flux fraction of the total POC flux measured by the traps varied from 3–5% (Table 4).

Furthermore, by continuously measuring the current speed and turbidity, with the RCM-9 instrument mounted on top of the lander, we could estimate the lateral transport of suspended particulate matter (SPM) at ~2.5 m a b during the deployments. The estimates were obtained by multiplying the current speed (cm s^{-1}) with the turbidity (mg l^{-1}); the turbidity sensor of the RCM-9 instrument being calibrated *in situ* with bottom water samples analysed for SPM at the same station. Lateral particle transport (g h^{-1} m^{-2}) was significantly higher during early spring compared to late summer, at least within the H-area (Table 1). Late summer values were similar for the H-area (317 ± 116 to 353 ± 183 g h^{-1} m^{-2}) and the K-area (310 ± 134 to 342 ± 123 g h^{-1} m^{-2}), but significantly lower at the deep T2 station (42 ± 27 g h^{-1} m^{-2}).

e. Macrofaunal biomass in the benthic chambers

Macrofauna were collected and analysed from 24 individual chamber incubations (Fig. 9). On the spring cruise macrofaunal biomass and abundance varied between 0.60–12.86 g dw m^{-2} (mean 5.68 ± 3.71 g dw m^{-2}, $n = 10$) and 3325–24600 indiv m^{-2} (mean 11785 ± 6731 indiv m^{-2}). A total of 151 taxa were identified of which Mollusca was the most dominant group in terms of biomass (45%) followed by Polycheata (34%), Echinodermata (16%), Miscellanea minor phyla (3%), and Crustacea (2%). The small bivalve *Abra nitida* was the single most abundant species encountered on the spring cruise, sometimes accounting for as much as 74% of the biomass in the chambers. Among the polycheates, *Ophelina cylindricata* and *Maldanidae* spp. belonged to the most abundant species. Late summer biomass values of ranged from 0.17–30.98 g dw m^{-2} (mean 5.90 ± 8.95 g dw m^{-2}, $n = 14$). Polycheata was clearly the dominating group of macrofauna on the late summer cruise (61%), followed by crustaceans (20%), echinoderms (13%) and molluscs (6%). The high SD between the chambers, during both seasons, indicated a nonnegligible spatial variability of the macrofaunal biomass distribution in these sedi-

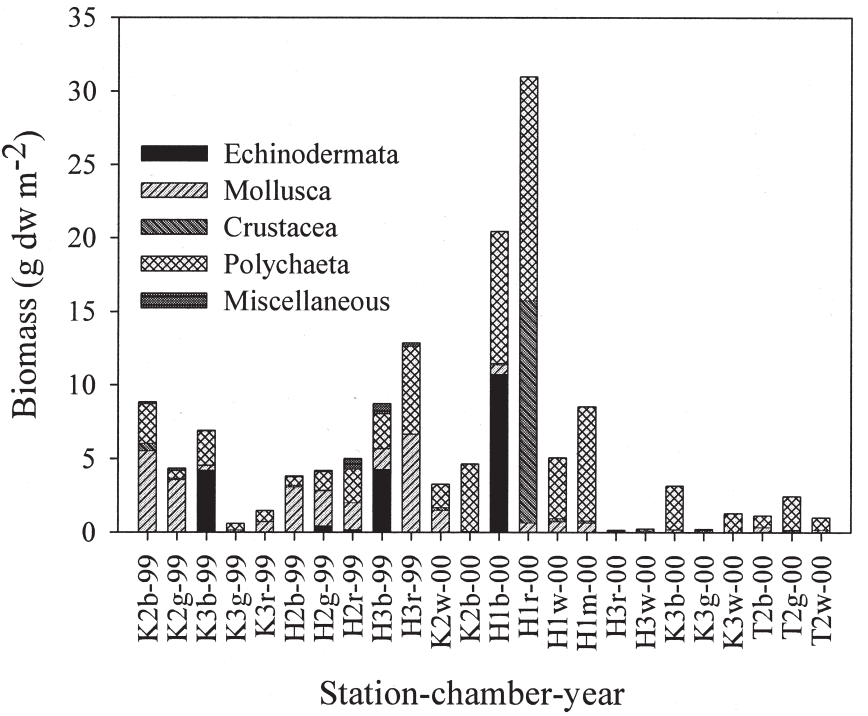

Figure 9. Macrofaunal biomass (g dw m^{-2}) in the individual benthic chambers. Each bar shows the distribution of the 5 taxonomic groups, Echinodermata, Mollusca, Crustacea, Polycheata and Miscellaneous minor phyla.

ments. On average 92% of the biomass in the chambers consisted of macrofauna >1 mm and 8% was between 0.5–1 mm, excluding the deep T2 station which made an exception with 48% >1 mm and 52% between 0.5–1 mm.

4. Discussion

a. Benthic respiration rates in the mesotrophic Skagerrak

The measured benthic oxygen uptake rates in this study showed good agreement with previous investigations made in the Skagerrak. Bakker and Helder (1993) obtained calculated O_2 fluxes from microelectrode measurements on deck from 26 stations, sampled over a large part of the Skagerrak, ranging from 2.6–17.9 mmol O_2 m^{-2} d^{-1}. *In situ* measured O_2 fluxes from three stations in the vicinity of the H- and T-area of this study, ranged from 11.8 to 16.1 mmol O_2 m^{-2} d^{-1} (Canfield *et al.,* 1993a). Furthermore, Hall *et al.* (unpublished results) measured O_2 fluxes, using both on deck- and *in situ* incubations, from 4.13 to 15.5 mmol O_2 m^{-2} d^{-1} on 12 different stations in the Skagerrak.

Although our range of oxygen flux values (1.89–24.8 mmol O_2 m^{-2} d^{-1}) span over a greater interval compared to previous studies, it should be pointed out that the highest flux

(24.8 mmol O_2 m^{-2} d^{-1}) is almost a factor of two higher than the second highest flux (13.9 mmol O_2 m^{-2} d^{-1}). Yet incubation data from this extreme flux value does not imply any malfunctioning of the oxygen electrode or any other obvious uncertainty allowing us to discard this value as erroneous. Few or no results are to our knowledge published on benthic C_{ox} rates in the Skagerrak. One of the few previous investigations of C_{ox} rates (Hall *et al.,* unpublished results) generated values over a range (3.26–18.1 mmol C m^{-2} d^{-1}) very similar to the one presented in this study (2.20–18.0 mmol C m^{-2} d^{-1}). Canfield *et al.* (1993a) determined total C_{ox} rates (10.2–15.7 mmol C m^{-2} d^{-1}) on the same three stations mentioned above by quantifying and adding the contribution to OC mineralization from each of the different electron acceptors O_2, NO_3^-, MnO_2, FeOOH and SO_4^{2-}. A number of studies have shown that temporal variations in POC fluxes to the sea floor can be accompanied with temporal variations in the sediment oxygen uptake rates both in the deep-sea (Pfannkuche, 1993; Smith *et al.,* 1992; Smith and Kaufmann, 1999) as well as in coastal and shelf areas (Bakker and Helder, 1993). In coastal and shelf environments temporal variations in the bottom water temperature can also influence the oxygen uptake rate due to influence on bacterial activity and bioirrigation (Andersen and Hargrave, 1984; Hall *et al.,* 1989). However, in this study the bottom water temperature was more or less constant (6.6–7.3°C) during both cruises and should not have caused any spatial and/or temporal variations of the oxygen uptake rate. On the other hand one would expect higher C_{ox} and O_2 uptake rates during early spring compared to late summer as a response to the significantly higher concentrations of labile organic carbon, indicated by Chl-*a*, measured in the sediment in March 1999. Surprisingly enough no significant statistical difference was found for either of these two rates between the seasons. Nor did we detect any significant spatial variability in the magnitude of the fluxes between the H- and the K-area during any of the two cruises.

There are several possible explanations to the lack of observed seasonal as well as large-scale spatial variability. For example, the observed phytoplankton spring bloom in the euphotic zone during the early spring cruise indicated that the fresh planktonic material found in the sediment arrived during or just prior to this cruise. Hence, if a time lag exists between the deposition and oxidation of organic material as suggested by Rudnick and Oviatt (1986), it is likely that the benthic community had not completely reached its maximum response to this input of phytodetritus. The variability between stations within each area (mesoscale) and even more so between the individual chambers (small-scale) within each station could have drowned the temporal and large-scale ($\gg$1 km) variability during this study. The RSD of the mean chamber flux within one deployment varied between 17–56% (max 104%, including the exceptionally high value of 24 mmol m^{-2} d^{-1}) for O_2 and 33–70% for C_{ox}. This small-scale variability can be due to several factors. Hammond *et al.* (1996) found that measurement uncertainties in the fits of concentration versus time plots and in the determination of overlying water heights in the chambers often contributed more to the variance of chamber fluxes (15–40% of the mean) than spatial variability on scales $<$1 km. However, uncertainties of the individual fluxes of O_2 and C_T in this study were in general small, on average 2% of the O_2 flux and 16% of the C_T flux.

The bottom topography may vary between the chambers during the same deployment resulting in different overlying water heights in the individual chambers. Hence, if the chamber stirring mechanism would create artificial resuspension in one of the chambers due to low overlying water height, this would most likely enhance the fluxes of O_2 and C_T in this chamber compared to the others. However, the visual inspection of each chamber upon recovery of the lander did not indicate such problems.

Another potential problem when performing *in situ* chamber incubations in extensively bioturbated sediments are animal burrows extending over lateral distances greater than the size of the chamber itself (Reimers *et al.,* 2000). Unless the connection with the outside is cut off by the chamber-wall, the burrow can serve as a bridging conduit through which bottom waters can be directly exchanged with the overlying water in the chamber. This bridging conduit would tend to minimize chemical changes in the overlying waters of the chamber giving a lower flux estimate compared to a chamber that did not include such burrows and thus leading to a greater variability between the chambers. The shallower a chamber penetrates into the sediment the greater this problem should become. Since the chambers of the Göteborg lander penetrated rather deep into the sediment (~20–25 cm) an animal burrow had to be more than 40 cm long to be able to connect the inside of the chamber with the ambient bottom water. Thus, bridging conduits should not have been a significant problem in this study.

Small-scale variations in the distributions of fresh organic material (e.g. phytodetritus) could cause patchiness in the microbial and faunal distributions, which in turn could affect the spatial homogeneity of the OC oxidation rates. The last alternative may be supported in this study by the large variations in macrofaunal biomass encountered in the separate chambers of individual deployments as well as by the variability in Chl-*a* observed in the top few cm of the sediment within each station, especially during the early spring cruise.

b. Apparent respiration ratios

Although oxygen uptake is the most common measure of total benthic mineralization (Pamatmat, 1977; Smith and Hinga, 1983) it has some limitations. When estimating organic carbon mineralization with oxygen uptake in sediments where anaerobic degradation of organic carbon predominates, for example in the Skagerrak (Canfield *et al.,* 1993a, b; Thamdrup and Canfield, 2000), it is based on the assumption that anaerobic respiration and reoxidation of inorganic reduced compounds (e.g. Mn^{2+}, Fe^{2+} and H_2S) with oxygen occur simultaneously in the sediment. However, if some reduced substances escape the sediment to the overlying water or get buried in the sediment (e.g. as FeS) before they are reoxidized or if methane ebullition occurs, there will be a decoupling between the oxygen uptake and the mineralization rate of organic carbon. These uncertainties can be overcome by measuring the C_T flux across the sediment-water interface followed by correction for calcium carbonate dissolution in the sediment to obtain the C_{ox} rate (Anderson *et al.,* 1986). This rate equals the total CO_2 produced by both aerobic and anaerobic degradation of organic carbon in the sediment, provided that methane production can be neglected. Anderson *et al.* (1986) showed that at 100% aerobic respiration the respiration ratio

(C_{ox}:O_2) ranged between 0.71–1.09 (excluding nitrification) and depending on the composition (e.g. lipids, carbohydrates) of the degrading organic matter. Although we measured both oxygen uptake and C_{ox} rates in this study we cannot conclude anything about the contribution from aerobic respiration alone to the total O_2 uptake. However, it is well known that a substantial part of the O_2 uptake is used to reoxidize reduced compounds in Skagerrak sediments (Canfield *et al.,* 1993a; Thamdrup and Canfield, 2000). Both biological and physical reworking of the sediment, through bioturbation and e.g. wind or current induced resuspension, are crucial factors enhancing the reoxidation rates of Mn^{2+}, Fe^{2+} and H_2S (Aller, 1982; Aller and Blair, 1996; Canfield *et al.,* 1993b; Jørgensen, 1996).

Thus, by looking at the C_{ox}:O_2 flux ratio (excluding oxygen consumption due to nitrification) we can estimate the extent of reoxidation of reduced inorganic compounds assuming that a ratio equal to 1 indicates a steady state situation in the sediment where anaerobic mineralization and reoxidation occurs simultaneously. We found a total mean apparent respiration ratio of 1.3 ± 0.5, indicating some long-term burial of reduced substances (such as Fe^{2+}, Mn^{2+}, S/HS^-) in Skagerrak sediments. This number is in good agreement with what Anderson *et al.* (1986) found in the Gullmar Fjord (1.3) but considerably smaller than the findings of Hargrave and Phillips (1981) who estimated this ratio to be ~4 in eastern Canadian subtidal marine sediment. Jørgensen and Revsbech (1989) on the other hand, concluded that the loss of reduced compounds was insignificant in Danish coastal sediments. Several studies (Luther *et al.,* 1991; Thamdrup *et al.,* 1994) have also shown a temporal uncoupling of anaerobic mineralization and reoxidation, possibly as a response to changes in supply of organic substrate or oxidants. The higher mean apparent respiration ratio in early spring (1.5 ± 0.6) compared to late summer (1.1 ± 0.3) could indicate that we have a faster reoxidation of reduced inorganic compounds in the latter case. A possible explanation for this could be that the fresh phytodetrital material, found in the sediment during the spring cruise, rapidly induced a significant anaerobic degradation of the material leading to a net temporary buildup of reduced inorganic compounds in the sediment. In late summer this pool may have been reoxidized to a greater extent thus giving a lower apparent respiration ratio. This explanation is strengthened by the significantly better correlation that was found between the individual C_{ox} rates and O_2 fluxes (corrected for nitrification) during late summer compared to early spring (Fig. 10).

c. Importance of the benthic DOC flux

The benthic flux of dissolved organic carbon is a poorly quantified component within sedimentary and oceanic carbon cycling. The importance of DOC relative to O_2 uptake rates and C_{ox} rates in marine sediments have been widely debated (e.g. Alperin *et al.,* 1999; Bauer *et al.,* 1995; Burdige *et al.,* 1992, 1999; Burdige and Homstead, 1994; Hall *et al.,* 1990; Hulth *et al.,* 1997; Jahnke, 1996; Martin and McCorkle, 1993; Skoog *et al.,* 1996; Ståhl *et al.,* 2004a).

Obtained DOC fluxes in this study, taking the influence of biodiffusion and bioirrigation into account, ranged from 0.2 ± 0.1–1.0 ± 0.2 mmol C m^{-2} d^{-1}. These fluxes are generally lower than fluxes measured in whole-core laboratory incubations from the

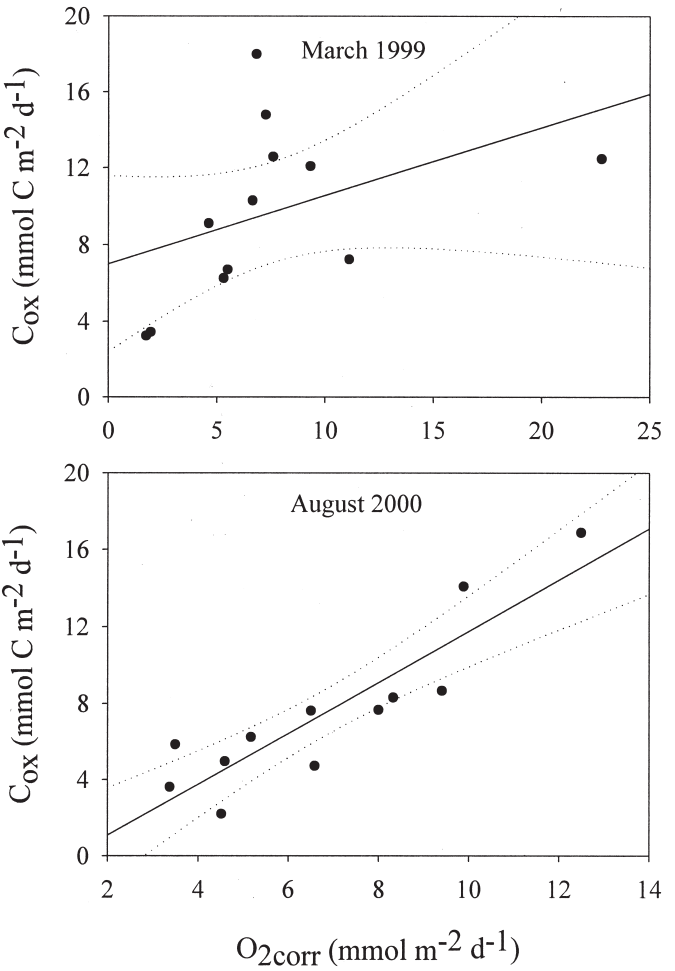

Figure 10. Correlation between C_{ox} rates and O_2 uptake rates (corrected for nitrification) in the individual chambers of the lander during spring (upper graph) and late summer (lower graph). Black lines indicate linear regression ($r^2 = 0.15$ [March 1999], 0.80 [August 2000]) and dotted lines are the 95% confidence interval.

estuarine Chesapeake Bay (Burdige and Homestead, 1994; 1.4–2.9 mmol C m^{-2} d^{-1}) but significantly higher than fluxes, calculated from pore water gradients, from the North Carolina continental slope (Alperin *et al.,* 1999; ~0.1 mmol C m^{-2} d^{-1}). They are in the lower range compared to *in situ* measured DOC fluxes, by benthic chambers, from the Gullmar Fjord (Skoog *et al.,* 1996; 0–2.5 mmol C m^{-2} d^{-1}) and from California continental margin sediments (Burdige *et al.,* 1999; 0.4–2.1 mmol C m^{-2} d^{-1}). Holcombe *et al.* (2001) investigated benthic DOC fluxes by several different methods in the oxygen minimum zone (OMZ) along the northwestern Mexican continental margin. They obtained pore water gradient calculated fluxes, from sliced and centrifuged sediment cores, ranging

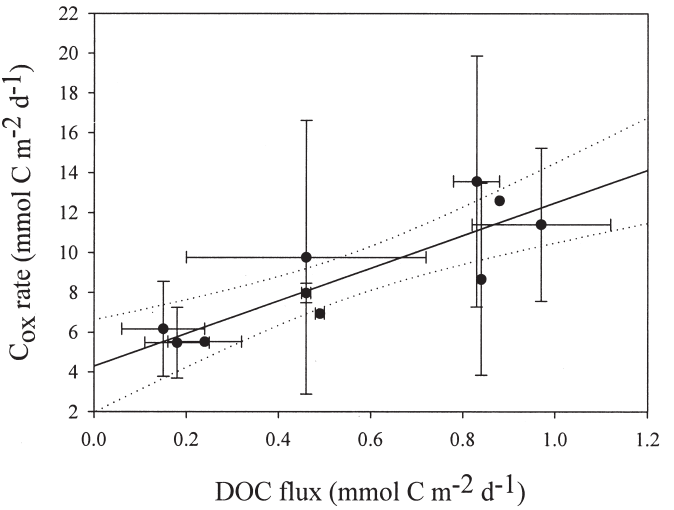

Figure 11. Correlation between the station mean C_{ox} rates (n = 1–4) and DOC fluxes (n = 2) from both seasons. Black line indicates linear regression (r^2 = 0.74) and dotted lines are 95% confidence interval. Error bars denote ±1 SD.

from 0.1–0.4 mmol C m^{-2} d^{-1} which agrees well with our range of values. Their total DOC fluxes, measured both *in situ* with benthic chambers as well as with whole-core incubations in the laboratory, gave only slightly higher values compared to the diffusive fluxes (0.3–0.6 and 0.2–0.5 mmol C m^{-2} d^{-1}, respectively), indicating that macrofaunal activity in the OMZ was minor.

The importance of the DOC fluxes in relation to the C_{ox} rates in this study (2–10%) is close to, or within the range of, all the above mentioned investigations (Burdige and Homestead, 1994, 3–13%; Skoog *et al.,* 1996, 0–18%; Alperin *et al.,* 1999, ~2%; Burdige *et al.,* 1999, <10%; Holcombe *et al.,* 2001, ~12%; Ståhl *et al.,* 2004a, 7–27%).

We found a significant (r^2 = 0.74, $P < 0.001$) linear correlation between the DOC fluxes and the C_{ox} rates (Fig. 11) in the Skagerrak, which supports the assumption that net DOC production rates are proportional to the overall sediment organic carbon remineralization rates (Alperin *et al.,* 1999). Furthermore, there was no significant correlation (r^2 = 0.3, P = 0.1) between the DOC flux as a fraction of the C_{ox} rate (DOC flux/C_{ox}) and the C_{ox} rate, which implies that the relative importance of the DOC flux did not change with increasing C_{ox} rate. Previous investigations (Burdige *et al.,* 1999; Burdige and Homstead, 1994) have shown nonlinear relationships between DOC fluxes and C_{ox} rates. The latter could be explained by that the flux data presented in these papers, in contrast to our data, spans over several orders of magnitude in flux. When calculating diffusive fluxes for DOC from pore water gradients one has to keep in mind that these fluxes may be subject to several potential sources of error. First of all DOC is composed of a complex and largely undefined mixture of organic compounds which makes it difficult to assign a correct D_{sed} (Martin and McCorkle, 1993). However, as Burdige *et al.* (1992) point out, the inverse

cube root relationship between DOC diffusion coefficients and molecular weights implies that a factor of ten range in the average pore water DOC molecular weight translates into only a factor of two uncertainty in the D_{sed}. Secondly, artefacts may be associated with sediment collection and isolation of pore water (Alperin *et al.,* 1999; Holcombe *et al.,* 2001; Jahnke, 1996; Martin and McCorkle, 1993). However, to avoid artefacts found due to the extraction technique and sample handling, all MUC-cores were immediately brought to a cold room upon recovery and sliced at *in situ* temperature followed by centrifugation at a low rpm (2100 for 30 min, ~600G) to avoid rupturing of cells.

Several studies (e.g. Alperin *et al.,* 1999; Burdige *et al.,* 1999; Burdige and Homstead, 1994; Holcombe *et al.,* 2001) have shown a good agreement between diffusive and measured fluxes (with benthic chambers) implying that, at least on those sites, the flux of DOC was controlled by molecular diffusion. However, the sediments of the Skagerrak are known to harbour an abundant macro- and meiofauna (e.g. DeBovee *et al.,* 1996; Josefson, 1981, 1985, 1986; Rosenberg *et al.,* 1996). Therefore, yet another potential source of error could be underestimation of the flux by only using Fick's first law since it does not include the influence of biodiffusion or bioirrigation, but only the diffusive flux across the sediment-water interface. To overcome this problem we calculated a biodiffusion/bioirrigation factor (α) by comparing chamber-measured total C_T fluxes with calculated diffusive fluxes of C_T, from pore water gradients. The α-factor ranged from 1.0–5.4 (mean: 2.2 ± 1.5, $n = 10$) depending on the station and season. It should also be mentioned that a similar comparison was made for dissolved silicate on the late summer cruise, generating a mean α-factor of 2.0 ± 0.5 ($n = 10$), which was in good agreement with the α-factor used to calculate DOC fluxes in this study. Other studies have found this factor to be 0.9–2.0 for C_T fluxes and 1.4–3.0 for O_2 fluxes in coastal Danish sediments (Andersen and Kristensen, 1991). Glud *et al.* (1998) showed that in shallow Arctic sediments the benthic *in situ* O_2 uptake was enhanced by a factor of 1.8–2.9 over the diffusive uptake of O_2 due to large densities of bioirrigating macrofauna. Rutgers van der Loeff *et al.* (1984) found this enhancement factor to be 2–10 for total silicate fluxes, compared to diffusive fluxes, from near-shore sediments of the Gullmar Fjord. All these α-factors obtained in previous studies of coastal and shelf sediments are similar to those we used.

d. Influence of POM quality on respiration rates

It is well known that particular organic material (POM) in the sediment consists of a complex mixture of more or less degradable fractions (Herman *et al.,* 2001) which are sequentially decomposed by microbial communities, with the more reactive substrates being consumed first (Westrich and Berner, 1984). Thus, one important factor in controlling the recycling efficiency of OC in marine sediments is the quality of the degrading organic matter. In other words labile material (e.g. phytodetritus) will have a greater effect on the OC recycling rates compared to more refractory bulk organic matter. In compliance with this, we found no significant relationships when correlating O_2 fluxes or C_{ox} rates with the bulk sedOC. This has previously been established for O_2 fluxes and sedOC in the Skagerrak by Bakker and Helder (1993). When correlating these fluxes against the more

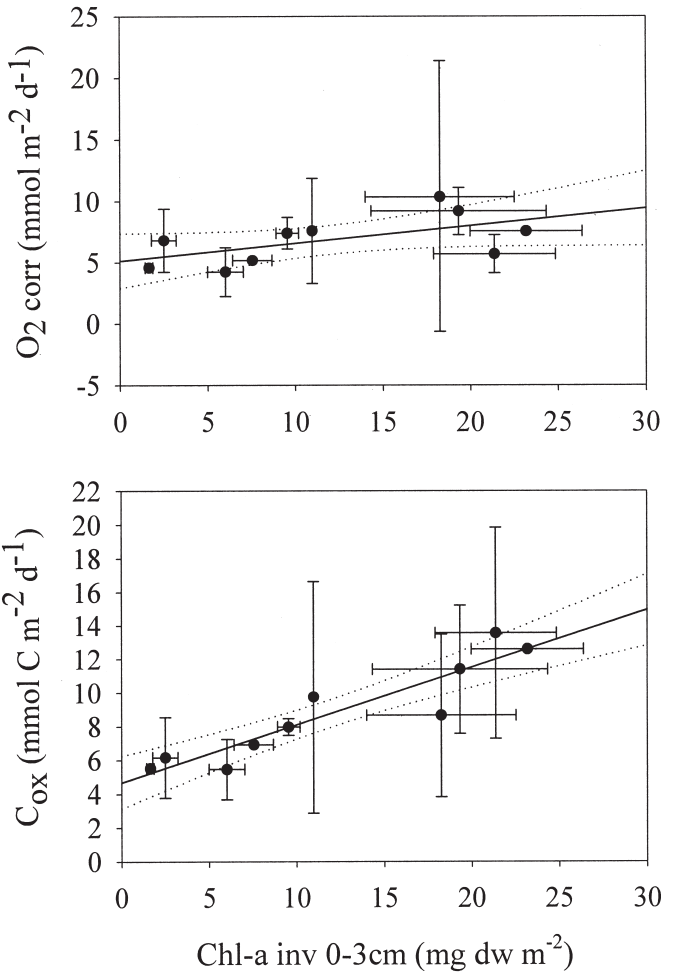

Figure 12. Station mean O_2 uptake rates (n = 1–4, upper graph), corrected for nitrification, and station mean C_{ox} rates (n = 1–4, lower graph) versus Chl-*a* inventory in the top 0–3 cm of the sediment from both seasons. Black line indicates linear regression (r^2 = 0.32 [O_{2corr}], 0.85 [C_{ox}]). Error bars denote ±1 SD.

labile fraction of OC, represented in this study by the Chl-*a* inventory in the 0–3 cm of the sediment, we obtained a weak correlation (r^2 = 0.3) for O_2 and a strong correlation (r^2 = 0.9) for C_{ox} (Fig. 12). This confirms that OC oxidation rates to a large extent were controlled by the availability of labile phytodetrital organic matter in these sediments. However, when correlating C_{ox} rates against deeper Chl-*a* inventories (e.g. 0–10 or 0–20 cm) we obtained poorer r^2 values (r^2 = 0.7 and r^2 = 0.5, respectively), indicating that the most reactive zone with regard to OC was close to the sediment-water interface. By converting the Chl-*a* inventory to phytoplankton carbon (Phyto-C), assuming that 1 g of Chl-*a* is equivalent to 60 g of planktonic carbon (Sun *et al.,* 1991), and then divide the

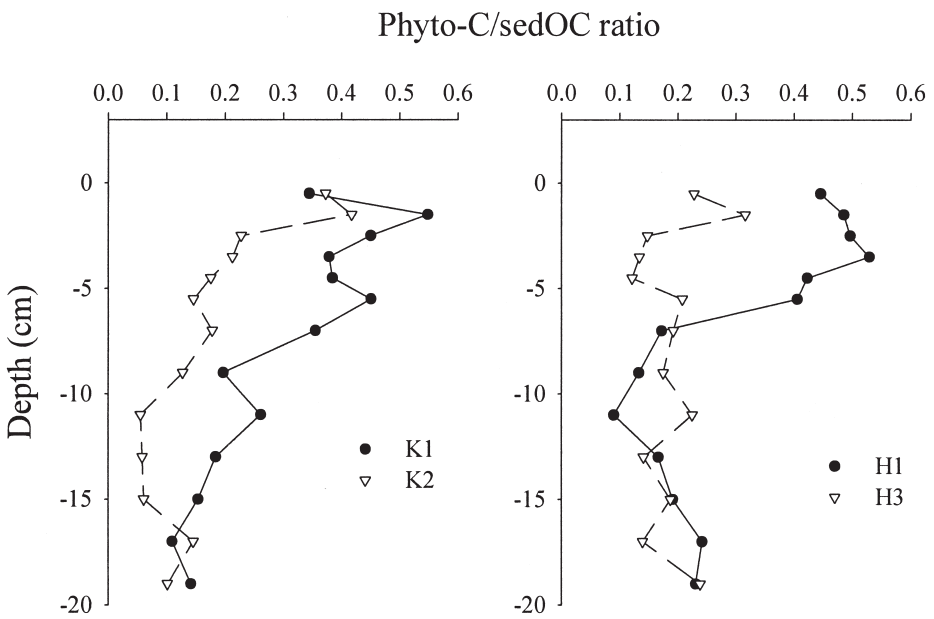

Figure 13. Examples from 4 different stations of Phyto-C:sedOC ratio with depth in the sediment.

obtained Phyto-C values with the bulk sedOC inventory, we could calculate the planktonic carbon fraction of the total OC pool, and how this fraction varied with depth (Fig. 13). The sharp sub surface maximum in the Phyto-C:sedOC ratio versus depth profile confirmed that the most reactive zone, i.e. where most of the OC oxidation occurred, was in the top 3 cm of the sediment. This gives a residence time for the phytoplankton carbon pool in the reactive zone of the sediment between 5.5–10.5 days in spring and 1.5–6.2 days during late summer (total mean: 6.2 $\pm$ 2.9 days).

A plausible explanation for the more obvious relationship between C_{ox} rates and Chl-*a* compared to O_2 fluxes and Chl-*a* (Fig. 12), is probably that organic matter degradation to a large extent is driven by anaerobic processes in Skagerrak sediments. This explanation is consistent with what was concluded in section b, i.e. that when anaerobic processes predominates in the sediment C_T fluxes (corrected for $CaCO_3$ dissolution) are a better estimate than oxygen uptake rates of the total organic carbon degradation.

e. Macrofaunal influence on organic matter degradation

Another important factor that can influence the rates of organic matter degradation is the presence of bioturbating and bioirrigating fauna. Although it is generally recognized that bacteria dominate the decomposition of organic material in marine sediments, there are many reports (e.g. Aller, 1982; Aller and Aller, 1998; Glud *et al.,* 1998; Kristensen and Blackburn, 1987; Rutgers van der Loeff *et al.,* 1984) suggesting that benthic macrofaunal activities, such as bioirrigation and bioturbation, can enhance degradation of biogenic

matter. Irrigation activities of macrofauna, taking place across the redox boundary in the sediment, can stimulate the reoxidation of reduced compounds in the anoxic zone and the exchange of metabolites between different zones, which may promote degradation rates of organic matter. Reexposure of old refractory organic matter from deeper anoxic sediment layers to oxic conditions, for example caused by bioturbation activities in the sediment, was shown by Hulthe *et al.* (1998) to promote degradation of this structurally complex material.

In the continental shelf, slope and deep-sea sediments of the northwestern Mediterranean, Tahey *et al.* (1994) found a positive correlation between macrofaunal density and enhancement of oxygen fluxes over what could be accomplished by molecular diffusion alone. Similar observations were made by Glud *et al.* (1994) comparing *in situ* measured oxygen fluxes with macrofaunal biomass in continental margin and deep-sea sediments off Namibia, South Atlantic. In this study however, macrofaunal biomass (dw) did not show any significant correlation with neither the O_2 fluxes nor the C_{ox} rates measured in the benthic chambers, which is in conformity with what Ståhl *et al.* (2004a) found in the oligotrophic northern Aegean Sea. Nor did flux data correlate with biomass of any of the individual taxonomic groups (Echinodermata, Mollusca, Crustacea, Polycheata, Miscellanea minor phyla). The lack of correlation may partly be explained by the fact that direct macrofaunal respiration rates have been shown to be small in comparison to their indirect stimulation of the bacterial respiration rates by bioirrigation and bioturbation activities (Forster and Graf, 1995; Vopel *et al.,* 2003). The latter is a function of e.g. the structure of the macrobenthic community, the size distribution, the geometrical shape of burrows, the modes of burrow ventilation and feeding strategies (Aller and Yingst, 1978). Thus, we conclude that biomass in itself is not a sensitive enough measure of macrofaunal influence on benthic OC remineralization rates, at least not in Skagerrak sediments. Furthermore, in contrast to the investigations of Tahey *et al.* (1994) and Glud *et al.* (1994), which were made from shallow to deep-sea sediments, the range of macrofaunal biomass and benthic respiration rates in this study may also have been too limited to be able to detect a significant correlation between them.

But the fact that measured C_T fluxes in this study were enhanced by 1.0–5.4 times over diffusive C_T fluxes, still implies that macrofauna have a significant influence on the exchange of OC remineralization products in Skagerrak sediments.

f. Benthic mass balances for organic carbon

One of the goals with this study was to investigate the importance of OC recycling and preservation in shelf and slope sediments of the Skagerrak compared to other coastal, continental margin and deep-sea sediments. As discussed above, we consider the corrected C_T fluxes to be a more reliable estimate of OC oxidation than oxygen uptake rates especially in sediments where anaerobic respiration predominates. Therefore, only the former rate is used in the benthic mass balances of OC as a measure of benthic respiration.

Before the deposited POC can undergo complete mineralization to CO_2/HCO_3^- it has to be hydrolyzed to DOC by extracellular enzymes in the sediment. If the DOC is not

Table 5. Benthic mass balances for OC at the individual stations during both seasons. The OC burial rate (OC_{burial}) is equivalent to the sediment accumulation rate (ω) multiplied with the bulk sedOC below the mixed zone. $OC_{recycling}$ denote $\Sigma(DOC_{flux} + C_{ox})$ at each station. The deposition rate of particulate organic carbon (POC_{input}) was calculated as $\Sigma(OC_{bur} + OC_{recycled})$, whereas the OC burial efficiency ($OC_{bur.eff.}$) was calculated as $(OC_{burial}/POC_{input}) \cdot 100$.

Stn/yr	ω (g cm^{-2} y^{-1})	OC_{burial} (mmol C m^{-2} d^{-1})	$OC_{recycled}$ (mmol C m^{-2} d^{-1})	POC_{input} (mmol C m^{-2} d^{-1})	$OC_{bur.eff.}$ (%)
K1/99	0.33	14.3	13.5	27.8	51
K2/99	0.63	27.3	14.4	41.7	65
K3/99	0.23	9.34	5.65	15.0	62
H2/99	0.22	6.27	12.4	18.6	34
H3/99	0.15	5.99	9.54	15.5	39
K2/00	0.63	27.3	10.2	*37.5 (47.8)	73
K3/00	0.23	9.34	6.73	*16.1 (39.3)	58
H1/00	0.40	8.94	6.32	*15.3 (63.0)	58
H3/00	0.15	5.99	8.43	*14.4 (57.1)	42
T2/00	0.12	6.54	5.21	*11.8 (14.3)	56

*Figures within brackets denote POC fluxes measured by the sediment traps (see Table 4).

mineralized immediately it can escape from the sediment both by molecular diffusion and through ventilation of bioirrigating fauna. In Skagerrak the calculated mean DOC efflux, taking the influence of biodiffusion and bioirrigation into account, was ≤10% of the C_{ox} rate. However, it was not insignificant and should therefore be included in the recycling rates of OC in order to make proper mass balances.

The recycling rates ranged from 5.2 mmol C m^{-2} d^{-1} at the central T2 station in August 2000 to 14.4 mmol C m^{-2} d^{-1} at the K2 station in March 1999 (Table 5). The obtained estimates of OC burial at each station showed that the northeastern K-area in general experienced higher OC burial rates (9.3–27.3 mmol C m^{-2} d^{-1}) compared to the southern H-area (6.0–8.9 mmol C m^{-2} d^{-1}). These results show good agreement with previous studies of burial fluxes in the Skagerrak. Anton *et al.* (1993) reported OC burial rates from the Skagerrak southern slope and basin of 7–11 mmol C m^{-2} d^{-1}, whereas burial rates in the eastern and northeastern part have been found to be between 10–36 mmol C m^{-2} d^{-1} (Jørgensen *et al.,* 1990; Meyenburg and Liebezeit, 1993; Per Hall, unpublished results). At the deep central T2 station the burial rate (6.45 mmol C m^{-2} d^{-1}) was somewhat higher than what have been previously measured in the same area (3–5 mmol C m^{-2} d^{-1}; Hall *et al.,* unpublished results).

Particulate organic carbon (POC) deposition rates were estimated by adding the burial rates and the recycling rates of OC, assuming steady state for the bacterial and faunal biomass pools in the sediment (Table 5). Since the recycling rates can vary on a seasonal scale whereas the burial rates integrate over a considerably longer time scale, a combination of these two rates will be associated with uncertainties. Nevertheless, this approach has often been used previously to estimate the POC deposition rate (Berelson *et al.,* 1996; Canfield, 1994; Hulth *et al.,* 1997; Martens *et al.,* 1992; Reimers *et al.,* 1992; Ståhl *et al.,*

2004a, b) although the DOC flux has previously rarely been considered when constructing such benthic mass balances. Holcombe *et al.* (2001) estimated that ~8% of the total carbon input to the sediment escaped as DOC and that this significant leak of energy had to be considered in the sedimentary carbon budget in order to fully understand the global carbon cycle. In this study, the mean DOC flux (0.6 ± 0.3 mmol C m^{-2} d^{-1}) constituted only ~3% of the calculated mean POC input (21.4 ± 10.6 mmol C m^{-2} d^{-1}, Table 5). The lower net loss of DOC to the overlying water implies a more effective mineralization, or possibly adsorption, of the total sedimentary production of DOC. This may be due to more oxygenated bottom waters and hence a more abundant macrofauna in Skagerrak sediments, compared to the western Mexican continental margin sediments studied by Holcombe *et al.* (2001).

The calculated mean POC deposition rate corresponds to 31–47% of the estimated annual primary production of 200–300 g C m^{-2} yr^{-1} on a basin-wide scale for the Skagerrak (Fonselius, 1995). These values agree well with the estimates of Wollast (1991), suggesting that 25–50% of the primary production settles on the sediment-water interface of continental shelves. However, and as discussed below, a major fraction of the POC deposited in Skagerrak sediments does most likely not originate from primary production in the Skagerrak.

The burial efficiencies (OC_{burial}/POC_{input}) varied between 34–73% (Table 5) with a total mean of 54 ± 12% for all stations. The K-area had in general higher OC burial fluxes than the H-area and the same pattern was observed for the burial efficiencies for which the K-area ranged from 51 to 73% (mean: 62 ± 8%) and the H-area from 34 to 58% (mean: 43 ± 10%). In the abyssal deep-sea and in some oligotrophic continental margin sediments, having very low sediment accumulation rates, only 0.1–5% of the deposited POC is preserved in the sediment (Canfield, 1994; Ståhl *et al.,* 2004a, b).

Compilations and evaluations of a large number of observations in many different seas have shown that the burial efficiency (or % organic carbon preserved) generally increase with increasing sediment accumulation rates (Canfield, 1989; Canfield, 1994; Henrichs and Reeburgh, 1987). In conformity with these findings we found a significant positive correlation ($r^2 = 0.62$, $P = <0.0001$) between the burial efficiencies and the sediment accumulation rates in the Skagerrak (Fig. 14). The obtained burial efficiencies are in the upper end of the range compared to several other continental margin and slope sediments, but so are the sediment accumulation rates (Table 6). Especially the northeastern K-area has a substantial degree of OC preservation compared to other slope and shelf environments with similar accumulation rates (Canfield, 1994; Glud *et al.,* 1998). Even the very fast accumulating (100 mm yr^{-1}), near-shore and organic rich (4–5% C) coastal sediments of Cape Lookout Bight, North Carolina, have burial efficiencies which are not higher than, but of the same magnitude as in the K-area (66–76%; Martens *et al.,* 1992). Hence, the high degree of OC carbon preservation observed in Skagerrak sediments, especially in the northeastern part, suggests that this part of the North Sea act as a considerable net sink for organic carbon, even in a global continental margin context (Table 5).

A plausible explanation for this effective preservation of OC could be strong lateral

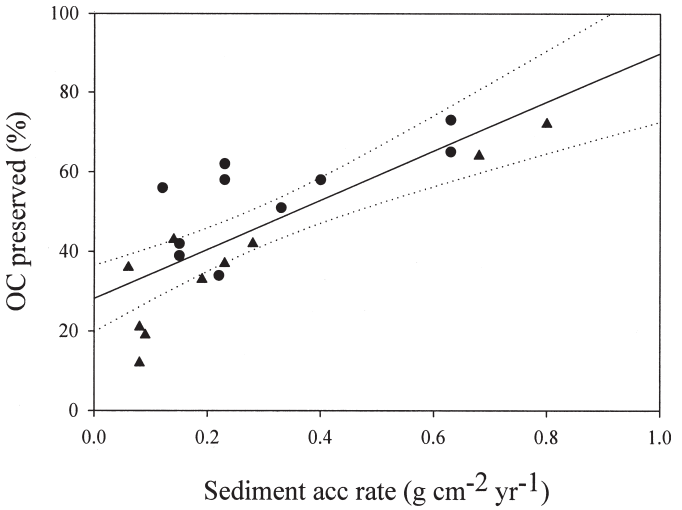

Figure 14. Burial efficiency or organic carbon preserved (%) versus sediment accumulation rate (g cm^{-2} yr^{-1}) from the respective stations in this study (●) and from other stations in the Skagerrak (▲) previously visited in 1992 and 1994 (Hall *et al.,* unpublished results). Black line indicates linear regression ($r^2 = 0.62$).

import of older more refractory POC from areas surrounding the Skagerrak. Several studies have suggested that the Skagerrak is the main depositional area for suspended organic and inorganic material transported with the currents from the North Sea and to some extent from the Baltic Sea making it the "dustbin" of the North Sea (Aure and Dahl, 1994; OSPAR, 1993; Van Weering *et al.,* 1987, 1993). This was partly confirmed by our current- and turbidity measurements made with the RCM-9 instrument (Table 1), indicating a significant lateral transport of SPM in both the H- and the K-area, but considerably less in the central deep part of Skagerrak. The amount of laterally transported SPM was of similar magnitude in the H- and the K-areas.

By comparing the calculated POC inputs from the mass balances with the POC caught in

Table 6. Examples of contrasting continental margin environments with regard to sediment accumulation rates and burial efficiencies.

Investigations	Area	Depth (m)	ω (g cm^2 y^{-1})	$OC_{bur.eff.}$ (%)
This study	Skagerrak	112–562	0.12–0.63	34–73
Ståhl *et al.* (2004a)	Agean Sea	80–354	$3–13 * 10^{-3}$	0.1–5
Glud *et al.* (1998)	Svalbard	115–329	0.10–0.47	19–47
Hulth *et al.* (1997)	Southern Weddell Sea	280–648	$1.2–6.0 * 10^{-4}$	12–43
Berelson *et al.* (1996)	Central California Borderland	781–3592	$0.11–1.1 * 10^{-3}$	2–49
Martens *et al.* (1992)	Cape Lookout Bight	6–10	3.82	66–76
Jahnke (1996)	Southern California Borderland	~900	0.02	43

the sediment traps mounted on the lander (Table 5, late summer values), it is obvious that the calculated POC demand from the sediment community was far less than what seemed to be supplied from the water column. Etcheber *et al.* (1996) showed that on continental margins deeper traps catch significantly more material than shallower ones in the same array, which is commonly ascribed to lateral inputs of suspended material (Timothy and Pond, 1997). Therefore, it seems reasonable to conclude that the discrepancy observed between the mass balance calculated and sediment trap measured POC inputs in this study was caused by laterally advected and resuspended material, a conclusion supported by our simultaneous current and turbidity measurements.

At stations K2 and K3 the calculated POC inputs were only 78% and 41%, respectively, of the measured POC fluxes in the sediment traps. On the H-stations this discrepancy was even greater (H1 = 24%, H3 = 25%). The deep central T2 station, however, experienced little lateral particle transport according to the current- and turbidity measurements (Table 1) and consistent with this also showed a better agreement between the POC input estimated from the mass balance and the sediment traps (83%).

Nevertheless, one has to keep in mind that the time-scales of these two measures are very different and therefore associated with uncertainties. The trap was operated on a daily basis whereas the calculated POC input represents time-scales from weeks with regard to recycling rates and many decades for sediment accumulation rates.

Although the amount of laterally transported suspended material was similar in the K- and H-areas, the discrepancy between the mass balance derived and trap derived POC input was lower in the northeastern area compared to the southern area. This fact, together with the fact that burial efficiencies were higher in the former than in the latter area, suggests that a larger fraction of the laterally transported material settled in the K-area compared to the H-area. Furthermore, the sediment trap data showed that the K-area had somewhat lower Phyto-C:POC ratios and higher C/N values than the H-area (Table 4), implying that the suspended organic material in the northeastern part of Skagerrak was of lower quality compared to the southern part of the Skagerrak. A likely explanation for these observations is that the laterally transported SPM has been deposited and subsequently resuspended several times on its way from the H-area to the K-area with the prevailing counterclockwise current direction in the Skagerrak, thus becoming more refractory over time. In other words, the reason why sediments in the northeastern Skagerrak act as a more effective OC sink may be that more organic matter and of lower quality is deposited there compared to the southern Skagerrak.

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