Impact of the burrow-dwelling polychaete *Nereis diversicolor* on the degradation of fresh and aged macroalgal detritus in a coastal marine sediment

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ABSTRACT: Impacts of the irrigating and detritus-feeding polychaete *Nereis diversicolor* on degradation of fresh and aged ^{14}C labeled *Fucus serratus* detritus deposited into sandy marine sediment were examined in microcosm experiments. The fate of detritus deposited at the surface or buried 3 cm into the sediment was followed over a period of 18 d. Fluxes of solutes (total labeled CO_2 [$T^{14}CO_2$] and labeled dissolved organic carbon [$DO^{14}C$]) across the sediment–water interface in the absence and presence of *N. diversicolor* were compared to changes in pool size and distribution of these solutes and labeled particulate carbon ($PO^{14}C$) within the sediment. The results showed that fresh detritus at the surface of defaunated sediment was degraded twice as fast as aged detritus (k_{POC} = 18×10^{-3} and 8×10^{-3} d^{-1}, respectively, where k is the decay constant). *N. diversicolor* increased the surface $PO^{14}C$ decay by 35 and 90 % for fresh and aged detritus, respectively. Competition for food between *N. diversicolor* and microorganisms reduced the microbial degradation of fresh detritus at the surface by 20 % compared with defaunated sediment. Enhanced microbial degradability after passage through the gut of *N. diversicolor* was probably responsible for a 20 % increase in microbial decay of surface-deposited aged detritus in faunated compared to defaunated sediment. The decay of subsurface-deposited fresh and aged detritus in defaunated sediment (k_{POC} = 10×10^{-3} and 3×10^{-3} d^{-1}, respectively) was ca. half of that for surface-deposited detritus. Activities of *N. diversicolor* (irrigation and feeding) increased the degradation of buried $PO^{14}C$ by 160 and 270 % for fresh and aged detritus, respectively. The irrigation-associated stimulation of microbial decomposition by injection of oxygen into and removal of toxic metabolites from sediment was 90 and 300 % for fresh and aged detritus, respectively. The several-fold enhancement of microbial decay of aged subsurface detritus substantiates the importance of burrow irrigation and oxygenation for degradation of otherwise refractory detritus in sediments. In the absence of irrigated burrows, a larger fraction of partly degraded detritus may remain undegraded and be buried permanently in the sediments.

KEY WORDS: *Nereis diversicolor* · Irrigation · Feeding · Decomposition · *Fucus serratus* · Detritus · Oxic/anoxic · Sediment

INTRODUCTION

Degradation of organic substrates in marine sediments occurs primarily near the sediment–water interface, and is mediated by an array of aerobic and anaerobic microbial processes, as well as detritivorous macrofauna (Lopez & Levinton 1987, Fenchel et al. 1998). The initial microbial decomposition of newly deposited organic matter occurs at the oxic sediment–water interface, where aerobic bacteria conduct complete degradation of organic carbon to CO_2 with oxygen as the electron acceptor. Deposit-feeding animals simultaneously meet their nutritional requirements by ingesting, digesting, assimilating and respiring some of the deposited organic matter and associated microorganisms (Tenore et al. 1982, Lopez & Levinton 1987). The nutritional value of detritus determines its availability to and utilization by deposit-feeders and microorganisms (Tenore et al. 1984).

Fresh detritus derived from phytoplankton and macro-algae can directly support detritivore and microbial growth, while aged detritus and detritus derived from vascular plants are less available for microorganisms, and not directly assimilable by most deposit-feeders (Findlay & Tenore 1982, Kristensen & Holmer 2001).

A large fraction of deposited organic matter escapes aerobic degradation and is buried into anoxic sediments by passive accretion or mixing by water currents and infaunal reworking (Rusch et al. 2001, Stoeck & Kröncke 2001). Anaerobic decomposition is accomplished here by mutualistic consortia of bacteria, because no single type is capable of complete carbon oxidation (Fenchel et al. 1998). Hydrolytic and fermenting bacteria first split polymeric organic molecules into smaller and water-soluble organic acids. These are then mineralized completely by respiring bacteria using a variety of oxidized inorganic compounds as electron acceptors (e.g. Fe[III] and SO_4^{2-}). However, unidirectional redox successions with depth are rare in coastal sediments. Oscillations between oxic and anoxic conditions caused by oxygen leaching from plant roots and irrigated animal burrows result in a temporal and spatial mosaic of microzones, with aerobic metabolism occurring in an otherwise anoxic sediment (Aller 1994, Holmer et al. 2002)

It is well established that benthic macrofauna enhance organic matter degradation in sediments. The magnitude of the faunal impact varies from a few percent in some cases to several hundred percent in many cases, and depends on the specific location, the sediment characteristics and organic matter supply, as well as the functional group, abundance and size of animals present (van Duyl et al. 1992, Banta et al. 1999, Kristensen 2000, 2001, D'Andrea et al. 2002). Burrow-dwelling animals affect microbial processes in 2 major ways: (1) translocation of particles between redox zones during feeding and burrowing activities, and (2) introduction of reactive electron acceptors (i.e. oxygen) into otherwise reduced sediment and removal of reduced metabolites via irrigation (Aller & Aller 1998, Kristensen 2000). Redox conditions appear to be crucial for the rate of microbial decay as fresh plant detritus is generally degraded equally fast under oxic and anoxic conditions, whereas aged detritus is degraded up to 10 times faster under oxic than anoxic conditions (Hulthe et al. 1998, Kristensen & Holmer 2001). A number of recent studies have therefore suggested that the oxidation of subsurface sediment via irrigation is more important for microbial degradation than the redistribution of particles by feeding and reworking activities (Banta et al. 1999, Furukawa et al. 2001, D'Andrea et al. 2002). Kristensen & Holmer (2001), for example, estimated that total sediment carbon oxidation is enhanced up

to 80% by irrigation, but only up to 10% by particle redistribution.

The faunal impact on microbial processes may not only depend on the type and age of organic matter present in the sediment, but also on interactions between animals and microorganisms. Thus, Kristensen et al. (1992) hypothesized that infaunal irrigation primarily enhances microbial degradation of relatively refractory detritus, while ingestion and metabolization by detritivores diminishes the role of bacteria in the degradation of freshly deposited and labile detritus. The interactions between detritivores and bacteria are probably related to competition for available food sources and animal predation on bacteria through more or less selective ingestion of detritus colonized by microorganisms (Lopez & Levinton 1987).

We believe that the ideas proposed by Kristensen et al. (1992) and others are important for our understanding of the biogeochemistry and food web dynamics of sedimentary environments. The purpose of this study was therefore to provide experimental verification of the impact of macrofaunal feeding and burrow irrigation on microbial degradation of fresh and aged plant detritus in coastal marine sediment. Our approach was to examine in detail the fate of fresh and pre-decomposed ^{14}C-labeled macroalgal (*Fucus serratus*) detritus, supplied to either the surface or 3 cm below the surface of sediment microcosms inhabited by the polychaete *Nereis diversicolor* over an 18 d period.

Nereis diversicolor was chosen for the experiments because it has proved to be an ideal model organism in bioturbation studies with a significant impact on sediment processes (Kristensen et al. 1992, Christensen et al. 2000, Kristensen 2001). Its widespread distribution along northern European coasts further substantiates the importance of this polychaete species in coastal areas. *N. diversicolor* lives in 5 to 10 cm deep U- or Y-shaped semi-permanent burrows at densities of up to 4000 ind. m^{-2} (Davey 1994). It feeds by scavenging all edible items (sediment detritus containing bacteria as well as dead and live animals and plants) around the burrow openings or by filtering suspended phytoplankton by the use of mucus nets (Vedel & Riisgård 1993, Nielsen et al. 1995). The burrow is frequently reconstructed and actively irrigated by dorso-ventral body movements at rates of up to 4 ml min^{-1} (equivalent to 10^3–10^4 l m^{-2} d^{-1} at the population level, Christensen et al. 2000).

MATERIALS AND METHODS

Sediment and worm collection. Sediment and specimens of *Nereis diversicolor* were collected in November 1998 from the shallow (0.2 to 0.6 m) oligotrophic

marine lagoon, Fællesstrand, at the NE tip of the island of Fyn, Denmark. The lagoon is sheltered from heavy wave action, but the upper few cm of the sediment are mixed by bioturbation and occasionally by wave-induced resuspension. The sediment is composed of well-sorted, organic-poor sand (17 to 20% water content, 0.4 to 0.6% organic content), with a median particle size of ~200 µm. The macrophyte flora is poor and dominated by patchy growth of *Ruppia maritima* along the coastline and scattered occurrence of drifting seaweed (*Fucus* sp.). Benthic microalgae (i.e. diatoms and filamentous cyanobacteria) are the most important primary producers in the lagoon. The benthic macrofauna is dominated by high numbers of *N. diversicolor*, *Corophium volutator*, and *Hydrobia neglecta*. For more details consult Kristensen (1993).

The uppermost 10 to 12 cm of sediment was dredged and sieved through a 2 mm mesh on location to remove macrofauna and larger particles. Intact specimens of *Nereis diversicolor* were collected simultaneously. The freshly sieved sediment was transferred into 24 acrylic core tubes (5.2 cm i.d., 30 cm long) to a depth of 20 cm, allowing a water column of ~10 cm. After return to the laboratory, 3 individuals of *N. diversicolor* (~400 mg each) were added to each of 12 cores (N-cores), equivalent to a density of 1400 ind. m^{-2} and a biomass of 565 g m^{-2} (fresh weight). The worms rapidly dug into the sediment and formed irrigated burrows within 1 d. The remaining 12 cores were used as defaunated controls (D-cores). The cores were subsequently allowed to acclimate for 6 d at 15°C in continuously aerated seawater tanks. Seawater with a salinity of 20 was supplied from the sampling area.

Preparation of ^{14}C-labeled *Fucus serratus*. Actively growing tips of the brown algae *F. serratus* were collected in September 1998 along the pier of Kerteminde Harbor on the east coast of the island of Fyn, Denmark. In the laboratory, the algal tips were placed under continuous light (Grolux, 200 µmol m^{-2} s^{-1}) for 7 d in trays containing 1 l of 18°C artificial seawater (salinity of 20) to which was added H^{14}CO$_3^-$ (1.1 MBq), NaNO$_3$ (500 µM), and KH$_2$PO$_4$ (50 µM). Sufficient new tissue was produced during the 7 d labeling period to ensure that the algal material used in the experiment was homogenously labeled with ^{14}C. The average weight gain of 4 portions of *F. serratus* tips was 23 ± 4%.

After incubation, the algal tips were washed in seawater and minced for 10 min in a kitchen blender. The material was subsequently sieved through 750 µm mesh to remove larger particles and rinsed with seawater in 63 µm mesh to remove dissolved carbon compounds. The resulting algal detritus was split into 2 portions. One portion with a molar C:N ratio of 17 and specific activity of 11.0 kBq mmol C^{-1} was frozen immediately for later use as 'fresh' (F) detritus. The

Table 1. Notation matrix of the 8 different treatments used in the experiment. Fresh (F) and aged (A) detritus were distributed at the surface ($_{surf}$) or 3 cm into subsurface ($_{sub}$) sediment of cores with (N) and without (D) *Nereis diversicolor*

	Fresh detritus	Aged detritus
Nereis-cores		
Surface	NF$_{surf}$	NA$_{surf}$
Subsurface	NF$_{sub}$	NA$_{sub}$
Defaunated cores		
Surface	DF$_{surf}$	DA$_{surf}$
Subsurface	DF$_{sub}$	DA$_{sub}$

other portion was pre-decomposed aerobically in seawater at room temperature for 55 d to ~60% of the original radioactivity. After centrifugation, the pre-decomposed detritus with a molar C:N ratio of 9 and specific activity of 10.6 kBq mmol C^{-1} was frozen for later use as 'aged' (A) detritus.

Experimental set-up. To each of 6 N-cores and 6 D-cores was added 1 g wet wt F detritus (~23.2 mBq m^{-2}), while to each of the remaining 6 N-cores and 6 D-cores 1 g wet wt A detritus was added (~22.8 mBq m^{-2}). The detritus was either spread evenly at the surface of the cores or buried at 3 cm depth. The subsurface addition was performed by carefully lifting the upper 3 cm of the sediment core while the detritus was applied. After settling of the detritus and repositioning of the upper 3 cm sediment, the cores were placed in closed incubation systems. The 3 cores of each of the 8 treatments (Table 1) were, for practical reasons, supplied with recirculating seawater from 1 common reservoir. Thus, each incubation system (Fig. 1) consisted of a
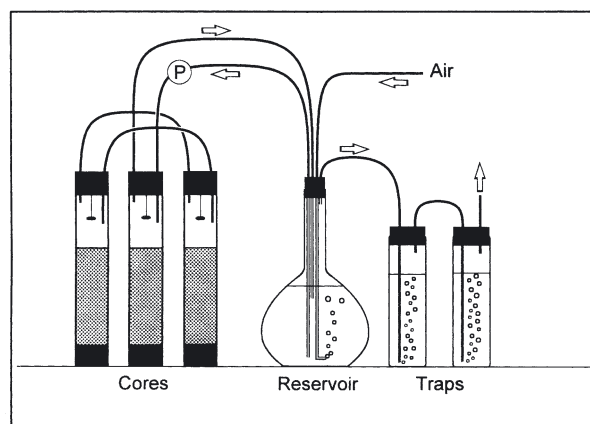

Fig. 1. Schematic presentation of the incubation system. Water flow (arrows) between sediment 'cores' and the seawater 'reservoir' is driven by a peristaltic pump (P). Flow (arrows) of moistened atmospheric 'air' is bubbled through the reservoir and subsequently through 2 NaOH traps

pump that supplied the overlying water of 3 cores individually (4 ml min^{-1}); a 2 l reservoir (renewed every third day), which supplied and received water passing the cores; and 2 NaOH traps (renewed every third day) where the air returning from the reservoir was stripped of all CO_2 (including $^{14}CO_2$). Each core was supplied with a rotating magnetic bar activated by an externally rotating central magnet (60 rpm) to maintain a homogeneous water phase. All incubation systems were kept in darkness at 15°C during the 18 d experimental period.

Flux measurements. The cumulated release of ^{14}C-labeled solutes ($^{14}CO_2$ and $DO^{14}C$) from the sediment in the 3 cores of each system was determined on a 3 d basis, with samples taken from the reservoirs and traps after every renewal. Samples of 5 ml from the reservoirs were transferred to 25 ml scintillation vials, mixed with 125 µl of 1 M NaOH and 15 ml of scintillation liquid, and counted on a Packard 2200 CA Tricarb scintillation analyzer for determination of total dissolved ^{14}C ($TD^{14}C_{reservoir}$). Other 5 ml reservoir samples were mixed with 250 µl of 0.5 M HCl. After purging with N_2 for 15 min to remove $^{14}CO_2$, the samples were mixed with 15 ml of scintillation liquid and counted for determination of dissolved organic ^{14}C ($DO^{14}C_{reservoir}$). The amount of $^{14}CO_2$ released by aeration of the reservoirs was quantified by determining the radioactivity of 5 ml samples from the NaOH traps after mixing with 15 ml scintillation liquid ($^{14}CO_{2trap}$). The total release of $^{14}CO_2$ from the 3 cores in each incubation system was:
$$T^{14}CO_2 = TD^{14}C_{reservoir} - DO^{14}C_{reservoir} + {}^{14}CO_{2trap}.$$

The exchange of TCO_2 across the sediment–water interface of individual cores was determined every third day. The closed-flow system was temporarily disconnected and 25 ml water samples were taken from each of the 24 cores before and after a 4 h incubation period. TCO_2 was analyzed by the flow injection/diffusion cell technique (Hall & Aller 1992).

Sediment handling and analysis. The vertical distribution of various carbon pools in the sediment was determined immediately after the final flux incubation. All cores were sectioned into depth intervals of 0–1, 1–2, 2–3, 3–4, 4–6, 6–8 and 8–10 cm. Worms were collected during sectioning and lyophilized. More than 70 % of the added worms were recovered. Filtered porewater was obtained by centrifuging the sectioned sediment in double centrifuge tubes equipped with GF/F filters at 1500 rpm ($375 \times g$) for 10 min, followed by analysis for $T^{14}CO_2$ and $DO^{14}C$ as described above. The particulate organic carbon content (labeled as well as unlabeled) of dried and ground subsamples of the sectioned sediment and recovered worms, as well as the original fresh and aged *Fucus serratus* detritus, was analyzed in a Hewlett-Packard 185B CHN analyzer. The ^{14}C content was obtained by trapping the

evolved $^{14}CO_2$ from the effluent gas after combustion in the CHN analyzer, using 2 NaOH traps similar to those mentioned earlier.

Respiration of *Nereis diversicolor* feeding on ^{14}C-labeled detritus. Four average-sized individuals of *N. diversicolor* (~400 mg) were transferred to each of 2 cylindrical chambers (8 cm diameter, 15 cm height). The chambers contained a 1 cm layer of Fællesstrand sediment mixed homogeneously with 2 g wet wt of either F or A detritus. The 2 chambers were maintained for 18 d in the previously described flow system. The worms were carefully removed from the sediment every third day for determination of CO_2, $^{14}CO_2$ and $DO^{14}C$ release. Exchange measurements were performed on individual worms in 35 ml stoppered glass bottles containing oxygen-saturated seawater. Worms were gently rinsed in seawater and placed in glass tubes of appropriate sizes (simulating burrows) before transfer to the incubation bottles. Initial and final water samples were taken from the bottles before they were stoppered and immediately after a ~4 h incubation period, respectively. The bottles were not stirred, but the irrigation activity of worms and gentle shaking of the bottles just before the final sampling assured sufficient mixing of the water. Worms were returned to the chambers immediately after measurements were taken. Water samples were analyzed for dissolved carbon as described above.

RESULTS

Visual observations

Nereis diversicolor clearly affected the distribution of detritus added to the sediment surface. Almost all visible detritus disappeared from the surface in NF_{surf} and NA_{surf} cores within the first 3 d, whereas a distinct layer remained at the surface in DF_{surf} and DA_{surf} throughout the entire experimental period. All N-cores appeared oxidized with clearly visible irrigated burrow structures to 8–10 cm depth. The sediment in D-cores, on the other hand, gradually turned black with time due to precipitation of iron sulfides, except for a thin (<1 cm) oxidized surface layer.

Labeled particulate organic carbon (PO^{14}C)

The vertical distribution of PO^{14}C derived from both fresh and aged *Fucus serratus* detritus showed similar patterns in all parallel treatments (Fig. 2). PO^{14}C in the 0 to 1 cm layer of defaunated sediment with detritus added to the surface accounted for 72 (DF_{surf}) and 66 % (DA_{surf}) of the total final PO^{14}C recovery. The content
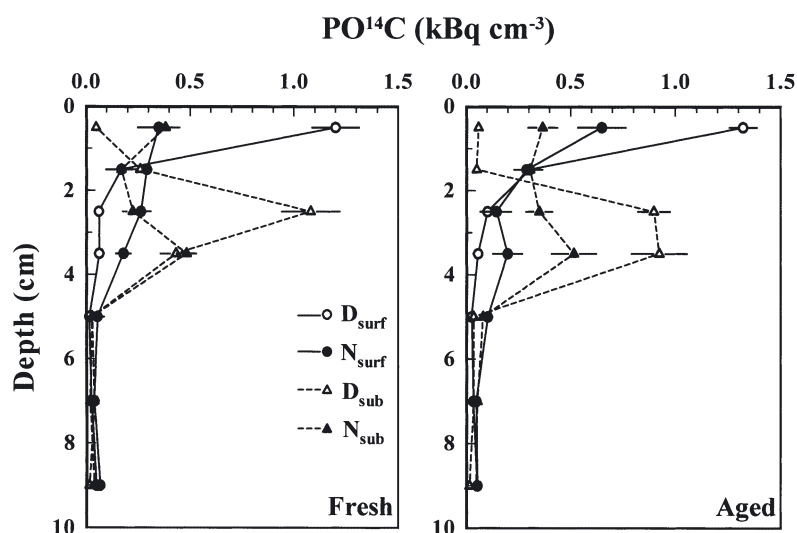
PO^{14}C (kBq cm^{-3})

Fig. 2. Vertical distribution of labeled particulate organic carbon (PO^{14}C) in defaunated (D) and *Nereis diversicolor* (N) sediment with detritus added to the surface ($_{surf}$) and 3 cm below the surface ($_{sub}$). Treatments with fresh detritus are shown in the left panel and aged detritus in the right panel. Results are given as the mean ± SE of results from 3 replicate cores

decreased gradually from 10 and 15%, respectively, at 1 to 2 cm depth, to <2% at 8 to 10 cm depth. When detritus was added at 3 cm depth in defaunated sediment, 76% (DF$_{sub}$) and 87% (DA$_{sub}$) of the total final PO^{14}C recovery was obtained from 2 to 4 cm depth. All other depth intervals only contained between 1 and 3%.

The burrowing activities of *Nereis diversicolor* smeared the PO^{14}C profiles considerably (Fig. 2). Only 25 (NF$_{surf}$) and 38% (NA$_{surf}$) of the total PO^{14}C recovery in sediment with detritus added to the surface was recovered in the 0 to 1 cm interval. However, each interval down to 3 to 4 cm depth in these sediments still contained more than 10% of the total PO^{14}C recovery. Subsurface deposited detritus was mixed almost homogeneously into the upper 4 cm of the sediment. Thus, only 49% (NF$_{sub}$) and 46% (NA$_{sub}$) of the PO^{14}C recovery was

found from 2 to 4 cm, whereas 27 and 19%, respectively, was mixed into the 0 to 1 cm layer.

The depth-integrated loss of PO^{14}C was strongly dependent on detritus age and treatment (Table 2). The disappearance of PO^{14}C during the experiment is assumed to follow a first-order exponential decay pattern according to: $G_t = G_0 \exp(-kt)$ (Berner 1980). The first-order decay constant (k) was estimated by selecting the initial PO^{14}C content as G_0 and the final PO^{14}C after $t = 18$ d as G_t. The decay of fresh detritus (14 to 39% loss, k = 9.9 to 26.2 × 10^{-3} d^{-1}) was generally 2 to 3 times faster than that of aged detritus (6 to 25% loss, k = 3.4 to 15.5 × 10^{-3} d^{-1}) (Fig. 3). Degradation was faster for surface-deposited than subsurface-deposited detritus in defaunated sediment (83% faster for fresh and 144% faster for aged detritus). However, the impact of detritus positioning was alleviated in the presence of *Nereis diversicolor*, where the difference of decay rates between surface and subsurface deposition was −7 and 23% for fresh and aged detritus, respectively. Accordingly, the impact of *N. diversicolor* on degradation was much stronger when detritus was deposited below the sediment surface (165 to 270%) than at the surface (35 to 87%). Furthermore, the stimulation of decay caused by *N. diversicolor* activities was more pronounced for aged than fresh detritus (i.e. 87 vs 35% for surface detritus and 270 vs 165% for subsurface detritus).

Labeled dissolved carbon (DO^{14}C and T^{14}CO$_2$) in porewater

The vertical distribution of dissolved ^{14}C compounds in the sediment was controlled by the position and age

Table 2. Budgets of ^{14}C in microcosms with and without the presence of *Nereis diversicolor* when fresh and aged *Fucus serratus* detritus is added to the sediment surface or buried 3 cm into the sediment. Values are given as mBq m^{-2} for an 18 d period. Microcosms were initially supplied with detritus containing 23.2 (F) and 22.8 (A) mBq m^{-2}. Values in parenthesis are given as % of added ^{14}C and sums up to recovery (%) as given at the bottom. pw = porewater

|	DF$_{surf}$	NF$_{surf}$	DF$_{sub}$	NF$_{sub}$	DA$_{surf}$	NA$_{surf}$	DA$_{sub}$	NA$_{sub}$
^{14}CO$_2$flux	4.88 (21)	5.89 (25)	2.74 (12)	6.77 (29)	1.87 (8.2)	2.63 (12)	0.56 (2.5)	2.54 (11)
DO^{14}Cflux	1.53 (6.6)	0.67 (2.9)	0.40 (1.7)	0.41 (1.8)	1.33 (5.8)	1.01 (4.4)	0.50 (2.2)	0.83 (3.6)
PO^{14}Cleft	16.78 (72)	14.07 (61)	19.91 (86)	14.36 (62)	20.08 (88)	16.89 (74)	21.03 (92)	18.00 (79)
PO^{14}Cworm	–	1.15 (5.0)	–	1.45 (6.3)	–	1.75 (7.7)	–	1.15 (5.0)
pwT^{14}CO$_2$	0.02 (0.1)	0.02 (0.1)	0.61 (2.6)	0.02 (0.1)	0.01 (0.1)	0.01 (0.1)	0.22 (1.0)	0.02 (0.1)
pwDO^{14}C	0.02 (0.1)	0.02 (0.1)	0.13 (0.6)	0.01 (0.1)	0.02 (0.1)	0.02 (0.1)	0.07 (0.3)	0.04 (0.2)
Total	23.23	21.82	23.79	23.02	23.31	22.32	22.38	22.58
Recovery (%)	100	94	103	99	102	98	98	99
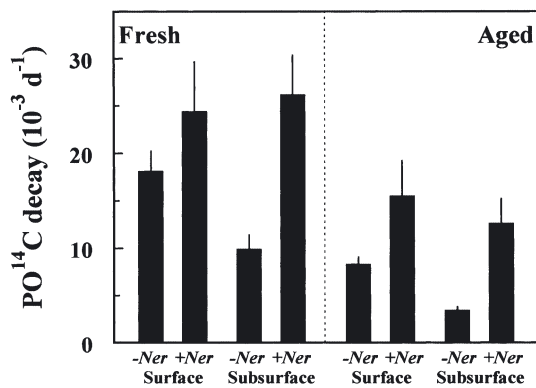
Fig. 3. Depth-integrated (0 to 10 cm) decay of labeled particulate organic carbon ($PO^{14}C$) in experimental cores with and without *Nereis diversicolor* (*Ner*). Values are given as decay constants (k), assuming exponential decay ($G_t = G_0 \exp[-kt]$; see 'Results' for details) over the 18 d period. Treatments with fresh and aged detritus are shown in the left and right panels, respectively. Values are given as the mean ± SE of results from 3 replicate cores

of ^{14}C labeled detritus, as well as the irrigation activity of *Nereis diversicolor*. Defaunated sediments with fresh detritus (DF_{surf} and DF_{sub}) showed pronounced accumulation of $DO^{14}C$ around the deposited detritus (Fig. 4) in a pattern similar to the $PO^{14}C$ distribution (Fig. 2). The equivalent sediments with aged detritus exhibited much lower (DA_{sub}) or missing (DA_{surf}) peaks of porewater $DO^{14}C$. The treatments with *N. diversicolor* generally showed no accumulation of $DO^{14}C$ at

any depth, irrespective of detritus type and positioning. The concentrations in these sediments were similar to those of DF_{surf} and DA_{surf} below 1 cm depth. The only exception was a minor peak at 2 to 4 cm depth in NA_{sub}.

Significant accumulation of porewater $T^{14}CO_2$ was only evident in defaunated sediment with subsurface detritus (DF_{sub} and DA_{sub}) (Fig. 5). The peak concentration at 2 to 4 cm depth was 2 times higher in sediment with fresh detritus than with aged detritus. High levels of $T^{14}CO_2$ were not constrained to the zone of detritus deposition, but extended throughout the examined sediment depth. All other treatments only showed trace amounts of porewater $T^{14}CO_2$ in the sediment. The depth-integrated accumulation of dissolved ^{14}C compounds in the porewater was insignificant compared to the initially added $PO^{14}C$ (Table 2). Except for $T^{14}CO_2$ accumulation in defaunated sediment with subsurface detritus (2.6% in DF_{sub} and 1.0% in DA_{sub}), the dissolved ^{14}C pools accounted for much less than 1% of the added $PO^{14}C$.

Flux of labeled dissolved carbon ($DO^{14}C$ and $T^{14}CO_2$)

The release of $DO^{14}C$ and $T^{14}CO_2$ from the sediment showed no specific pattern with time in any of the treatments after the first 3 d incubation period. The daily rates are therefore presented as the average of 5 time points, each consisting of a 3 d incubation period (Fig. 6). The initial 3 d incubation period is excluded due to handling inconsistencies. The impact of detritus quality on $DO^{14}C$ flux was generally insignificant, whereas the efflux of $T^{14}CO_2$ was 2 to 5 times higher in treatments with fresh than aged detritus. The release of $DO^{14}C$ was highest when detritus was added to the surface of defaunated sediment, but $DO^{14}C$ release, cumulated over the entire experimental period in these treatments, only accounted for 6.6 (DF_{surf}) and 5.9% (DA_{surf}) of the initially added $PO^{14}C$ (Table 2). The presence of *Nereis diversicolor* reduced the efflux of $DO^{14}C$ from surface-deposited detritus by 56 (NF_{surf}) and 24% (NA_{surf}). The $DO^{14}C$ release from subsurface-deposited detritus was only 26 (DF_{sub}) and 38% (DA_{sub}) of that from surface-deposited detritus. There was no impact of *N. diversicolor* on $DO^{14}C$ flux from subsurface-deposited fresh detritus (NF_{sub}), whereas a 66% increase occurred for aged detritus (NA_{sub}). Despite the limited or even negative effect of *N. diversi-*
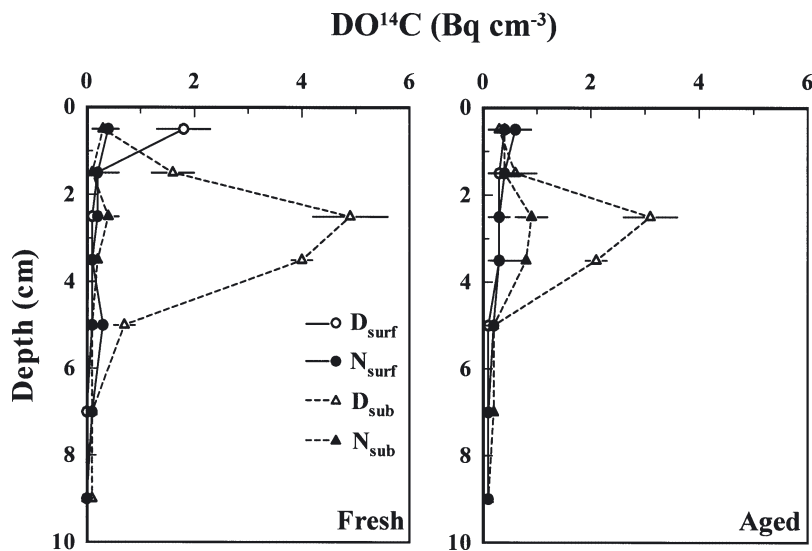

Fig. 4. Vertical distribution of labeled dissolved organic carbon ($DO^{14}C$) in defaunated (D) and *Nereis diversicolor* (N) sediment with detritus added to the surface ($_{surf}$) and 3 cm below the surface ($_{sub}$). Treatments with fresh and aged detritus are shown in the left and right panels, respectively. Results are given as the mean ± SE of results from 3 replicate cores
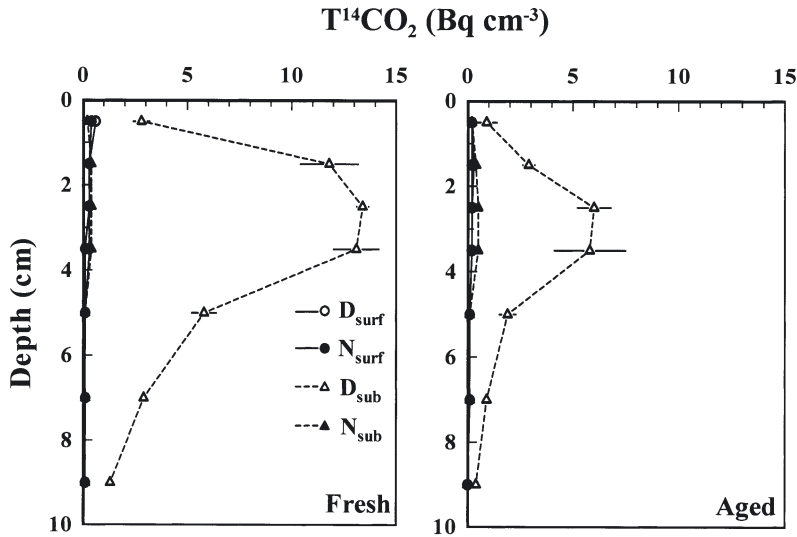
$T^{14}CO_2$ (Bq cm^{-3})

Fig. 5. Vertical distribution of labeled total CO_2 ($T^{14}CO_2$) in defaunated (D) and *Nereis diversicolor* (N) sediment with detritus added to the surface ($_{surf}$) and 3 cm below the surface ($_{sub}$). Treatments with fresh and aged detritus are shown in the left and right panels, respectively. Results are given as the mean ± SE of results from 3 replicate cores

color, direct excretion by the worms accounted for a substantial fraction of the $DO^{14}C$ efflux (Table 3), particularly when fresh detritus was added to the sediment (70 to 90%).

The pattern of $T^{14}CO_2$ release in the various treatments (Fig. 6) was a mirror image of the $PO^{14}C$ decay (Fig. 3), indicating that most of the lost detrital carbon was mineralized completely. The cumulated $T^{14}CO_2$ release over the entire experimental period accounted
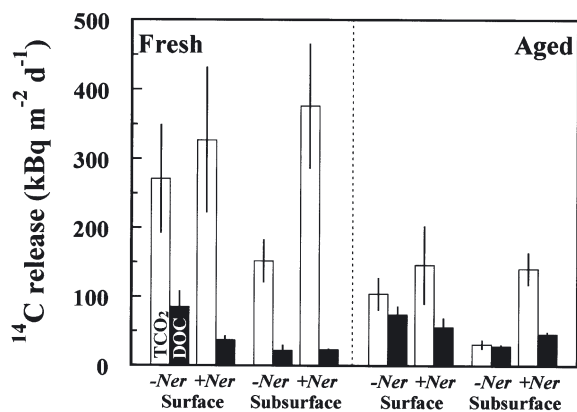

Fig. 6. Daily release of labeled total CO_2 ($T^{14}CO_2$) and dissolved organic carbon ($DO^{14}C$) from the sediment in experimental cores with and without *Nereis diversicolor* (*Ner*). Open and solid bars represent $T^{14}CO_2$ and $DO^{14}C$, respectively. Treatments with fresh and aged detritus are shown in the left and right panels, respectively. Values are given as average ± SE of 5 time points, each based on a 3 d incubation period

for 12 to 29% for fresh detritus and 3 to 12% for aged detritus of the initially added $PO^{14}C$ (Table 2). The highest release occurred in sediment with fresh detritus and *Nereis diversicolor* (NF_{surf} and NF_{sub}), and the lowest in defaunated sediment with aged detritus (DA_{surf} and DA_{sub}). Addition of detritus to the surface of defaunated sediment increased the $T^{14}CO_2$ efflux by 78 (DF_{surf}) and 234% (DA_{surf}) compared with subsurface-deposited detritus. The relative impact of *N. diversicolor* on $T^{14}CO_2$ release from surface-deposited detritus appeared independent of detritus quality and was limited to 21 (NF_{surf}) and 41% (NA_{surf}), whereas a more pronounced faunal effect was evident for subsurface-deposited detritus, particularly for aged material (NA_{sub}, Table 4), with a 354% increase compared with 147% for fresh material (NF_{sub}). Respiration of ingested ^{14}C-labeled detritus by *N. diversicolor* accounted for 23 to 31 and 12 to 13% of the $T^{14}CO_2$ release when fresh and aged detritus was added, respectively (Table 3).

Total CO_2 flux

The release of TCO_2 from the sediment (Fig. 7) followed the same general pattern among treatments as found for $PO^{14}C$ decay (Fig. 3) and $T^{14}CO_2$ release (Fig. 6). Thus, *Nereis diversicolor* increased TCO_2 flux by 51 (F_{surf}) and 149% (A_{surf}, Table 4). Respiration by worms accounted for 34 to 49% of the TCO_2 efflux (Table 3), with the highest contribution occurring when fresh detritus was added to the surface. However, the difference in TCO_2 release between various treatments (fresh vs aged detritus and surface vs subsurface deposition) containing *N. diversicolor* was small, and in defaunated treatments there was only a noteworthy difference between fresh and aged detritus (DF_{surf}:DA_{surf} = 1.6) when added to the surface.

Table 3. Contribution of *Nereis diversicolor* metabolism to the release of dissolved carbon species from the sediment. Results are given as % of total efflux

	CO_2	$^{14}CO_2$	$DO^{14}C$
NF_{surf}	48.7	31.2	67.6
NF_{sub}	33.6	23.4	91.3
NA_{surf}	36.0	12.3	21.4
NA_{sub}	35.0	12.8	26.1

Table 4. Stimulation of sediment rates (total CO_2 and $^{14}CO_2$ flux, microbially derived CO_2 and $^{14}CO_2$ flux [when worm metabolism is substracted], and $PO^{14}C$ decay) by the presence of *Nereis diversicolor*. Results are given as % change relative to the corresponding treatments without *N. diversicolor*. Abbreviations as in Table 1

	Total CO_2	Total $^{14}CO_2$	Micr. CO_2	Micr. $^{14}CO_2$	$PO^{14}C$ decay
F_{surf}	51	21	−23	−17	35
F_{sub}	115	147	42	89	165
A_{surf}	149	41	59	23	87
A_{sub}	128	354	49	297	270

Table 5. Contribution of added and indigenous detritus to the release of TCO_2 from the sediment. Values for added detritus are estimated by converting measured $T^{14}CO_2$ release to TCO_2 using the specific activity of 11.0 and 10.6 kBq mmol C^{-1} for fresh and aged detritus, respectively. Values for indigenous detritus are calculated as the difference between measured TCO_2 release (Fig. 7) and estimated contribution from added detritus. The units are mmol m^{-2} d^{-1} and values in parentheses indicate the percentage contribution. Abbreviations as in Table 1

	Added detritus	Indigenous detritus
DF_{surf}	25.3 (46)	29.2 (54)
NF_{surf}	30.6 (37)	51.7 (63)
DF_{sub}	14.2 (30)	33.5 (70)
NF_{sub}	35.1 (34)	67.5 (66)
DA_{surf}	9.7 (28)	24.4 (72)
NA_{surf}	13.6 (16)	71.3 (84)
DA_{sub}	2.9 (8)	34.7 (92)
NA_{sub}	13.2 (15)	72.9 (85)

The contribution of carbon from ^{14}C-labeled detritus to the TCO_2 efflux can be estimated as the measured $T^{14}CO_2$ flux divided by the specific activity of the detritus. The higher reactivity of organic carbon in fresh detritus is substantiated by a 30 to 46% contribution to the TCO_2 flux (Table 5). Although aged detritus contributed only 8 to 28% to the TCO_2 flux, it was still more reactive on a weight basis than the indigenous detritus, as the added detritus only accounted for ~3% of the total organic pool. The detritus contribution to TCO_2 flux was highest when the detritus was added to the surface of defaunated sediment, intermediate for bioturbated sediments, irrespective detritus positioning, and lowest when detritus was buried into defaunated sediment.

DISCUSSION

The aging procedure employed in the present study apparently removed a large fraction of the most labile pool of particulate organic carbon in *Fucus serratus*

detritus, as indicated by 30 to 60% lower reactivity of aged than fresh detritus in the various treatments (Fig. 3). A similar change in reactivity has been reported for lignin-rich barley hay after 50 d of aging, whereas the protein-rich diatoms apparently retain almost the same reactivity even after 40 d of aging (Kristensen & Holmer 2001). Decay characteristics of various materials are therefore operationally defined, and the final reactivity after aging depends on the type of substrate used as well as the duration of decay. As most organic materials exhibit an exponentially decreasing decay pattern through time (Westrich & Berner 1984), the actual attenuation is very dependent on the chemical composition of the substrate and the conditions under which the processes proceed (Fenchel et al. 1998). In any case, the results obtained in the present study suggest that the 2-fold difference in reactivity between fresh and aged *F. serratus* detritus is sufficient to determine the differential impact of burial and bioturbation on decay dynamics of labile and refractory components.

Although much of the leachable and fast-degrading DOC fraction in the *Fucus serratus* detritus was removed during the initial mincing and sieving procedure, the $DO^{14}C$ release after deposition at the sediment surface still accounted for up to 30 and 90% of the $T^{14}CO_2$ release from fresh and aged detritus,
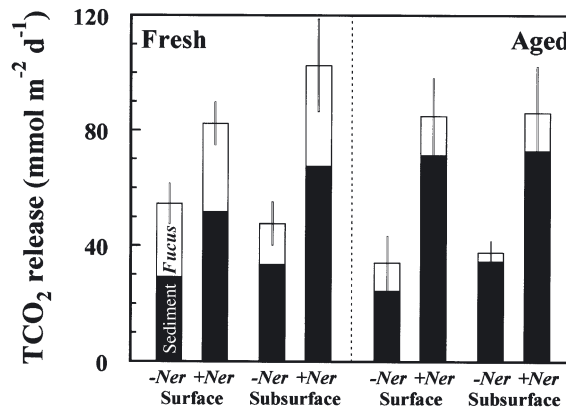

Fig. 7. Daily release of total CO_2 (TCO_2) from the sediment in experimental cores with and without *Nereis diversicolor* (*Ner*). The upper open part of the bars represents TCO_2 derived from added *Fucus serratus* detritus, and is estimated from $T^{14}CO_2$ data (Fig. 6) and the specific activity of the detritus. The lower solid part of the bars represents TCO_2 derived from the indigenous organic matter in the sediment. Treatments with fresh and aged detritus are shown in the left and right panels, respectively. Results are given as the mean ± SE of results from 3 replicate cores

respectively (Fig. 6). Much of this may be of secondary origin and result from dissolution of the particulate phase by the action of microbial exoenzymes (Madigan et al. 2002), with a significant contribution from excretion by worms when they are present. However, oxidation by the microbial communities within the sediment reduced the contribution of $DO^{14}C$ efflux to 10 and 40% of the $T^{14}CO_2$ efflux when detritus was deposited into the sediment. It is interesting that the absolute rates of $DO^{14}C$ release were almost identical in treatments with fresh and aged detritus. Consequently, the $DO^{14}C$ released from fresh detritus must be more available to respiring microorganisms than $DO^{14}C$ released from aged detritus. The pool of more refractory $DO^{14}C$ that escapes microbial oxidation before it is released to the overlying water, on the other hand, is of comparable size, irrespective of detritus type. Thus, the balance between net production of labile and refractory DOC and the time allowed for oxidation within the sediment determines the efflux of DOC, as argued by Burdige (2002).

Fate of surface-deposited detritus

As oxygen usually penetrates a few mm by diffusion into the surface of most coastal sediments (Jørgensen & Revsbech 1985), the initial microbial degradation of detritus at the sediment surface should largely be mediated by aerobic bacteria. The decay rates of fresh and aged *Fucus serratus* detritus deposited at the surface in the absence of *Nereis diversicolor* (decay constants: $k = 18 \times 10^{-3}$ and 8×10^{-3} d^{-1}, respectively; Fig. 3) are comparable to those previously reported for non-leachable particulate plant materials in oxic marine sediments (10 to 20×10^{-3} d^{-1}; Kristensen & Holmer 2001, D'Andrea et al. 2002), and substantiates that a significant fraction of surface-deposited detritus in the defaunated sediment was indeed degraded aerobically.

The 50 to 150% enhancement of TCO_2 efflux by *Nereis diversicolor* (Table 4) are within the range previously found for this species in sandy coastal sediments (Hansen & Kristensen 1997, Banta et al. 1999, Heilskov & Holmer 2001). The larger direct contribution of respiration by *N. diversicolor* to the TCO_2 efflux from the sediment (35 to 50%, Table 3) than values of ~20% as previously reported (Banta et al. 1999, Christensen et al. 2000) may be due to the relatively large biomass of worms added to the microcosms (565 g wet wt m^{-2}) compared to the natural abundance (80 to 230 g wet wt m^{-2} at Fællesstrand; Kristensen 1993). However, the faunal impact on degradation of *Fucus serratus* detritus deposited at the surface was modest, as the $T^{14}CO_2$ release was only increased by ca. 20 and 40%; and $PO^{14}C$

removal stimulated by ca. 35 and 90% (decay constants of 24×10^{-3} d^{-1} and 15×10^{-3} d^{-1}) for fresh and aged detritus, respectively (Table 4). As the indigenous detritus accounted for 50 to 60% of the total flux with fresh detritus and 70 to 80% with aged detritus added to the surface (Table 5), the enhancement of TCO_2 efflux by *N. diversicolor* was primarily driven by degradation of this carbon source (80 and 190% increase, respectively). The mechanism by which *N. diversicolor* affects surface-deposited detritus is primarily related to feeding and burrowing activities, as indicated by the rapid displacement of *F. serratus* detritus from the surface and down to at least 5 cm depth (Fig. 2). *N. diversicolor* either pulls edible detritus into burrows for later ingestion, or ingests the detritus right at the surface (Goerke 1971, Esselink & Zwarts 1989, Thomas & Blair 2002). The undigested remains are later defecated within burrows or occasionally at the surface.

Ingestion of labeled detritus by *Nereis diversicolor* clearly occurred, as 5 (fresh) and 8% (aged) of the recovered ^{14}C at the end was directly associated with worms (Table 2). If all this ^{14}C was incorporated and transformed into new worm tissue with an efficiency of 25% (Cammen 1980), worm respiration should account for 16 and 24% of the added fresh and aged *Fucus serratus* carbon, respectively. Since these estimates (equivalent to 58 and 200% of the measured $T^{14}CO_2$ efflux) exceed the measured contribution of *N. diversicolor* respiration (31 and 12%, respectively, Table 3), much of the $PO^{14}C$ associated with *N. diversicolor* is probably undigested *F. serratus* detritus remaining in the intestine. Based on the measured respiration and the incorporation efficiency mentioned above, the amount of *F. serratus* carbon converted into *N. diversicolor* tissue during the 18 d period was only 2.8 and 0.5% of the added fresh and aged detritus, respectively. For comparison, Josefson et al. (2002) found that deposit-feeders incorporate ca. 5% of ^{14}C-labeled fresh diatoms over a period of 54 d. Undigested material in the intestine must therefore account for 47 and 94% of the *F. serratus* carbon recovered from *N. diversicolor*. In other words, each 400 mg worm contained 8 mg fresh detritus or 25 mg aged detritus in the intestine at the end of the experiment. Although deposit feeders' digestive fluids are better able to solubilize sedimentary food substrates than are sedimentary extracellular enzymes (Mayer et al. 1997), the low assimilation and incorporation of aged detritus substantiates that the lower microbial degradability of aged compared to fresh detritus also corresponds to the digestibility of these substrates within worm intestines. Accordingly, Ahrens et al. (2001) found that *N. succinea* assimilated live phytoplankton with an efficiency of 55 to 95%, while bulk sediment organic matter was assimilated with an efficiency of only 5 to 18%.

Competition for food between detritivores and bacteria is known to occur after deposition of fresh detritus to sediment systems (Kristensen et al. 1992, Findlay & Watling 1998). Tenore et al. (1982) suggested that deposit feeders and bacteria compete for labile detritus, while bacteria regulate the availability of more refractory detritus to animals. A competitive interaction is also apparent between *Nereis diversicolor* and microorganisms when microbial degradation in faunated sediments is estimated by subtracting the measured metabolic contribution of *N. diversicolor* from the total carbon oxidation, particularly where fresh *Fucus serratus* is added to the surface (Table 4). Despite an increase in the total degradation of fresh *F. serratus* detritus, competition with *N. diversicolor* reduces the microbial contribution by ~20% compared with defaunated sediment. Direct feeding on *F. serratus*, and subsequent respiration by *N. diversicolor*, is therefore responsible for the increased $T^{14}CO_2$ release in this treatment. The modest but significant 20% increase in microbial oxidation of carbon from aged *F. serratus* in faunated sediment may be a consequence of the feeding activities by *N. diversicolor*. Maceration during ingestion, passage through the gut, and contact with digestive enzymes probably facilitate microbial attacks on otherwise refractory compounds after defecation. A similar increase in microbial degradability of refractory detritus by macrofaunal feeding activities has been observed on several occasions (Hargrave 1976, Horng & Taghon 2001, Kristensen & Pilgaard 2001). However, the stimulatory effect of *N. diversicolor* on microbial decay of aged detritus may also partly be due to increased oxygen exposure resulting from worm activities, such as irrigation (see next section below).

Fate of subsurface-deposited detritus

Microbial decay of detritus deposited 3 cm into defaunated sediment must occur by hydrolysis/fermentation coupled with anaerobic respiration (Fenchel et al. 1998). The electron acceptor in question is primarily SO_4^{2-}, because O_2 and NO_3^- do not penetrate to 3 cm depth, and most reducible Mn and Fe disappears within a few days in anoxic sandy sediment devoid of macrofauna (Epping & Helder 1997, Meyer et al. 2001, Kristiansen et al. 2002). The decay constant of subsurface deposited fresh *Fucus serratus* detritus ($k = 9.9 \times 10^{-3}$ d^{-1}) in defaunated sediment is almost 3 times higher than that of aged detritus (3.4×10^{-3} d^{-1}, Fig. 3). Comparable decay constants have previously been found for macrophyte detritus under anoxic conditions in laboratory experiments (Kristensen & Holmer 2001) and for metabolizable particulate

organic matter in anoxic Chesapeake Bay sediments (Roden & Tuttle 1996).

The decay rates for both types of detritus in anoxic subsurface sediment are about half of those obtained for detritus deposited in oxic surface sediment. If enhanced decay at the surface is caused by exposure to oxygen, the observed difference is relatively modest compared to the results of Kristensen & Holmer (2001). They found that the difference between oxic and anoxic decay of fresh and aged hay was a factor of 2 and 5, whereas the difference was a factor of 7 and >10 for fresh and aged diatoms. Hulthe et al. (1998) observed a similar difference between oxic and anoxic degradation of sediment detritus under *in situ* conditions. Furthermore, the trend for relatively faster decay of aged than fresh *Fucus serratus* detritus at the sediment surface compared with subsurface-deposited detritus is less than the differential oxygen effect found by Kristensen & Holmer (2001). These discrepancies suggest that surface-deposited detritus was not completely exposed to oxygen. The penetration of oxygen by diffusion from the overlying water was probably limited to the uppermost layer (i.e. less than 1 mm) of the actively degrading surface detritus, while the remainder was exposed to anoxic conditions. Degradation utilizing other electron acceptors than oxygen at rates comparable to those in subsurface sediment may therefore have prevailed in the deeper part of the detritus layer near the sediment surface, as previously observed for defaunated sediments covered by layers of *Ulva lactuca* (Nedergaard et al. 2002).

The presence of *Nereis diversicolor* in sediment with subsurface-deposited *Fucus serratus* detritus had a dramatic effect on detritus decay. The $PO^{14}C$ decay constants increased by 160 and 270% (26×10^{-3} d^{-1} and 13×10^{-3} d^{-1}) for fresh and aged detritus, respectively, and reached levels comparable to faunated sediment with surface-deposited detritus. A similar trend was observed for $T^{14}CO_2$ release, showing 150 and 350% increase, respectively. However, the distinct effect of *N. diversicolor* on degradation of fresh and aged detritus buried in the sediment was not reflected in the release of TCO_2, which was only enhanced by 115 and 130%, respectively. As the TCO_2 release was mostly derived from indigenous detritus (65 to 90%, Table 5), the large enhancement of $T^{14}CO_2$, particularly for aged detritus, is concealed by a more modest 100 to 110% increase in degradation of indigenous detritus.

Burrowing and feeding by *Nereis diversicolor* affect the distribution and degradation of subsurface-deposited detritus. The distinct inventories of $PO^{14}C$ observed at the location of deposition in defaunated sediment are not evident in faunated sediment, where $PO^{14}C$ is mixed more or less homogeneously into the

upper 4 cm. Particle-reworking activities primarily enhance the microbial degradation when detritus is occasionally exposed to oxygen at the surface. Otherwise the particles are just displaced within the sediment column and only affect the internal distribution of bacterial numbers and activity (Stoeck & Kröncke 2001) without any significant effect on the overall degradation. *N. diversicolor* have certainly also selectively ingested subsurface deposited detritus, as 6 and 5% of the total recovery of ^{14}C at the end of the experiment was associated with the worms (Table 2). From the measured respiratory release of $^{14}CO_2$ by *N. diversicolor* (23 and 13% of the total release from the sediment in treatments with fresh and aged detritus), and using the same calculations as above, ca. 60 to 70% of ^{14}C associated with *N. diversicolor* was undigested remains in the intestine. This is equivalent to ca. 12 mg detritus of both types in the intestine of a 400 mg worm.

As the direct contribution by *Nereis diversicolor* feeding, assimilation and respiration appears comparable in sediments with surface and subsurface detritus, most of the stimulation by *N. diversicolor* on the decay of subsurface detritus must be related to indirect effects on microbial activities. The most likely cause for the enhanced microbial decay of subsurface-deposited detritus is related to the vigorous burrow irrigation conducted by *N. diversicolor*. Its intermittent and forceful irrigation injects oxygen into subsurface sediment and removes potentially toxic metabolites from the porewater (Kristensen 2001). The strong advective transport caused by *N. diversicolor* irrigation is evident from the porewater profiles of $T^{14}CO_2$ (Fig. 5) and $DO^{14}C$ (Fig. 4). The distinct and large subsurface peaks of these solutes observed in defaunated sediment have almost disappeared in the faunated sediment. A similar rapid exchange of porewater solutes has been observed in a variety of sediments affected by infaunal irrigation (e.g. Banta et al. 1999, D'Andrea et al. 2002). The resulting injection of oxygen and associated redox oscillations are important for the heterotrophic microbial communities and enhances decomposition of particularly aged detritus buried in otherwise anoxic sediment (Aller 1994, Hulthe et al. 1998, Kristensen 2000). In accordance, the microbial decay of fresh and aged detritus buried in the sediment was increased by 90 and 300%, respectively. The much stronger enhancement of microbial degradation of aged than fresh detritus by oxidizing activities of *N. diversicolor* fully supports the predictions of Kristensen et al. (1992) and Kristensen & Holmer (2001).

The several-fold higher stimulation of microbial decay of aged detritus substantiates the importance of burrow irrigation for degradation of old and partly degraded detritus in sediments. If no injection of oxy-gen occurs, a larger fraction of these refractory compounds will remain undegraded and be buried permanently in sediments. As a consequence, the capacity for organic matter decomposition is increased dramatically in irrigated sediments.

CONCLUSIONS

Nereis diversicolor significantly increases the decay of fresh and aged *Fucus serratus* detritus in sediment. The direct and indirect effects of *N. diversicolor* on microbial activities are strongly dependent on the quality (age) of the detritus and its position (depth) in the sediment, and constrain the role of various activities (e.g. burrowing, feeding and irrigation). The impact of burrowing and feeding is related to redistribution of detritus and competition with the microbial community, as well as ingestion, assimilation and respiration by the animals. When detritus is moved between the oxic surface layers and anoxic subsurface layers of the sediment during burrowing, microbial decomposition shifts between an inefficient anaerobic and a more efficient aerobic metabolism. The microbial contribution to the decay of fresh detritus positioned at the surface is actually affected negatively by competition from *N. diversicolor*, when it feeds directly on this attractive detritus and associated microorganisms. No such competition occurs in the presence of aged detritus. On the contrary, microbial degradability of aged materials is enhanced after passage through the gut of *N. diversicolor*. Irrigation, on the other hand, primarily stimulates the decay of aged detritus buried into the sediment. The irrigation impact is of indirect nature and is caused by stimulation of microbial activity due to the increased availability of oxygen in subsurface sediment. The generally stronger enhancement of aged than fresh detritus decay by activities of *N. diversicolor* corresponds with the contention that the effect is primarily caused by injection of oxygen via irrigation, as argued by Kristensen & Holmer (2001), and fully supports the original ideas of Kristensen et al. (1992).

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