Impact of polychaetes (*Nereis* spp. and *Arenicola marina*) on carbon biogeochemistry in coastal marine sediments†

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Review

Known effects of bioturbation by common polychaetes (*Nereis* spp. and *Arenicola marina*) in Northern European coastal waters on sediment carbon diagenesis is summarized and assessed. The physical impact of irrigation and reworking activity of the involved polychaete species is evaluated and related to their basic biology. Based on past and present experimental work, it is concluded that effects of bioturbation on carbon diagenesis from manipulated laboratory experiments cannot be directly extrapolated to *in situ* conditions. The 45–260% flux (*e.g.*, CO_2 release) enhancement found in the laboratory is much higher than usually observed in the field (10–25%). Thus, the faunal induced enhancement of microbial carbon oxidation in natural sediments instead causes a reduction of the organic matter inventory rather than an increased release of CO_2 across the sediment/water interface. The relative decrease in organic inventory (G_b/G_u) is inversely related to the relative increase in microbial capacity for organic matter decay (k_b/k_u). The equilibrium is controlled by the balance between organic input (deposition of organic matter at the sediment surface) and the intensity of bioturbation. Introduction of oxygen to subsurface sediment and removal of metabolites are considered the two most important underlying mechanisms for the stimulation of carbon oxidation by burrowing fauna. Introduction of oxygen to deep sediment layers of low microbial activity, either by downward irrigation transport of overlying oxic water or by upward reworking transport of sediment to the oxic water column will increase carbon oxidation of anaerobically refractory organic matter. It appears that the irrigation effect is larger than and to a higher degree dependent on animal density than the reworking effect. Enhancement of anaerobic carbon oxidation by removal of metabolites (reduced diffusion scale) may cause a significant increase in total sediment metabolism. This is caused by three possible mechanisms: (i) combined mineralization and biological uptake; (ii) combined mineralization and abiogenic precipitation; and (iii) alleviation of metabolite inhibition. Finally, some suggestions for future work on bioturbation effects are presented, including: (i) experimental verification of metabolite inhibition in bioturbated sediments; (ii) mapping and quantification of the role of metals as electron acceptors in bioturbated sediments; and (iii) identification of microbial community composition by the use of new molecular biological techniques. These three topics are not intended to cover all unresolved aspects of bioturbation, but should rather be considered a list of obvious gaps in our knowledge and present new and appealing approaches.

Introduction

It has long been recognized that activities of macrobenthic organisms have significant effects on sediment–water solute exchange and diagenetic reactions within sediments. Much experimental and modelling work done over the years on the effects of reworking and irrigation by burrowing animals such as polychaetes, crustaceans and bivalves[1-5] have not only enhanced our understanding of bioturbation effects, but also provided important knowledge on general mechanisms controlling diagenetic processes in sediments. It is now well established that the distribution of a porewater solute is determined by the balance between transport and reaction processes, and that irrigating infauna may change this balance dramatically by enhancing transport conditions. This has been modelled by a variety of excellent models such as the cylinder model of Aller[6] and the non-local exchange model of Emerson.[7] Although these two models basically are equivalent,[8] the construction of the cylinder model allows the incorporation of additional realistic complexity (*e.g.* semipermeable burrow linings and periodic irrigation).

Nevertheless, the real complexity created from a multitude of behavioural activities by the wide variety of burrow-dwelling animals found in marine sediments is extremely difficult to describe mathematically. Activities, such as filter- or suspension-feeding and specific locations of faecal pellet deposition, may have serious impact on diagenetic reactions and solute distributions within sediments.[9] While models may improve our general knowledge on bioturbation effects, the particular activity of any specific assembly of infauna can only be determined by examining both the impact of each individual species as well as of the entire community.

This paper attempts to review the current knowledge on the impact of common intertidal polychaetes, *Nereis* spp. and *Arenicola marina*, on fluxes and reaction rates involving carbon in coastal sediments. The behaviour and life habits of these animals are linked to measured fluxes and porewater profiles of CO_2 as well as carbon reaction rates within sediments. The results are also used for the construction of simple (conceptual) models describing the impact of these species on carbon diagenesis in sediments. Finally, some guidelines are given for

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future work still needed to provide a more complete understanding of sediment carbon biogeochemistry and microbiology associated with *Nereis* spp. and *A. marina*.

Biology of *Nereis* spp. and *Arenicola marina*

Nereis spp.

The closely related polychaetes *Nereis diversicolor* (Fig. 1) and *N. virens* (Fig. 2) are widely distributed inhabitants of shallow silty and sandy sediments along Northern European coasts. Adult individuals of *N. diversicolor* are rarely longer than 15 cm whereas adult *N. virens* may occasionally exceed 50 cm in length. In accordance, the normal density ranges from 500 to 1000 individuals m^{-2} for *N. virens* and 3000 to 4000 individuals m^{-2} for *N. diversicolor*.[10] The small and opportunistic *N. diversicolor* is usually confined to a refuge in the intertidal zone by interspecific aggressions from the larger and competitively superior *N. virens*. Thus, fluctuations in salinity and temperature restrict the landward distribution of the relatively stenohaline and stenothermic *N. virens*, while competition restricts the seaward distribution of the euryhaline and eurythermic *N. diversicolor*.[10]

They both live in semi permanent U- or Y-shaped burrows in the sediment (Fig. 3). Through time, burrows may develop into multibranched structures extending to 20 cm depth for *N. diversicolor* and >40 cm depth for *N. virens* with numerous openings at the sediment surface.[12,13] The inhabitants ventilate their burrows vigorously from head to tail by undulatory body movements.

The two *Nereis* species have been described as omnivores and detritivores feeding by swallowing surface sediment as well as plant and animal remains around the burrow opening.[14] However, *N. diversicolor* also has the ability to live as a suspension-feeder.[15] The ventilatory water current is then driven through a mucus net spun by the worm near the entrance. Suspended food particles are retained in the net, which is subsequently eaten. No such suspension feeding has been observed in *N. virens*.

Fig. 1 *Nereis diversicolor* crawling at the sediment surface.

Fig. 2 *Nereis virens*. Head and first 16 segments.

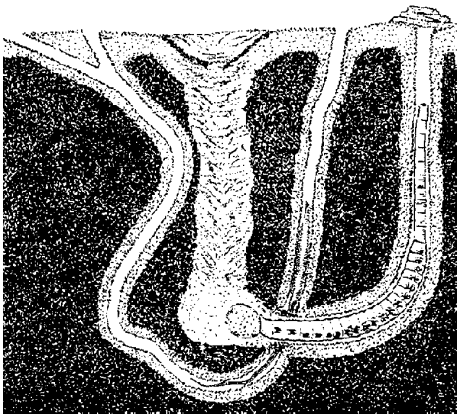

Fig. 3 Drawing of *Nereis* sp. and *Arenicola marina* in burrows. The dark areas represent reduced sediment and the light areas represent oxidized sediment (modified from Kristensen *et al.*[11]).

Fig. 4 *Arenicola marina* lying on the sediment surface.

Arenicola marina

The lugworm *Arenicola marina* (Fig. 4) is abundant on the lower intertidal zone in sandy to muddy-sand sediments along most Western European coasts. It is particularly abundant in the Wadden Sea where the density of lugworms frequently exceeds 50 individuals m^{-2}.[16,17] Adults have a body length of 15 to 25 cm, but individuals as long as 36 cm have been recorded.[18]

A. marina lives head-down in 20 to 40 cm deep J-shaped burrows in the sediment (Fig. 3). It ingests deep subsurface sediment and defecates at the surface.[19] As a result, the sand above the head sinks downward forming a feeding funnel. During defecation, the worm moves backwards until the tail reaches the sediment surface where it ejects a characteristic "worm-like" faecal cast (Fig. 5). Since *A. marina* ingests

Fig. 5 Sediment inhabited by *Arenicola marina* with numerous feeding funnels and faecal casts at the surface. Inset shows a close up of faecal casts.

sediment of low nutritive value, it must handle large amounts to satisfy its metabolic needs. It is generally believed that *A. marina* assimilates living bacteria, microphytobenthos, microfauna, meiofauna as well as digestible detritus associated with the sediment sinking down the feeding funnel.[18,20]

Burrow ventilation by *A. marina* is driven from tail to head by peristaltic movements of the body. Water enters the burrow through the tail opening to the surface and exits by percolation into the sediment in front of the head and up through the feeding funnel.[21]

Bioturbation mechanisms

The activities of benthic fauna have profound impact on physical, chemical and biological conditions in aquatic sediments. Sediment reworking and water irrigation (or ventilation) displaces both particles and porewater within the sediment.[22] By volume, the amount of water moved is much larger than that of particles, and burrows act as channels for the direct communication between subsurface porewaters and overlying water. The enhanced solute exchange, therefore, redistributes dissolved reactants and products of microbial reactions within sediments.[23,24]

Irrigation (ventilation)

Most infaunal animals actively irrigate their burrows with oxygen-rich overlying water. The renewal of burrow water serves important transport functions for the animals, such as supply of oxygen, removal of toxic metabolites and providing suspended food items. However, burrow irrigation may also affect the distribution of meiofauna and microorganisms, as well as the associated biogeochemical processes within the sediment.[4,5,25]

The irrigation of *Nereis* and *Arenicola* is intermittent with active and quiescent periods in a more or less rhythmic fashion. *N. virens* is active for about 20% of the time with 5–10 min irrigation periods followed by 20–30 min inactivity[26] (Fig. 6). *N. diversicolor* is considerably more active, particularly when it

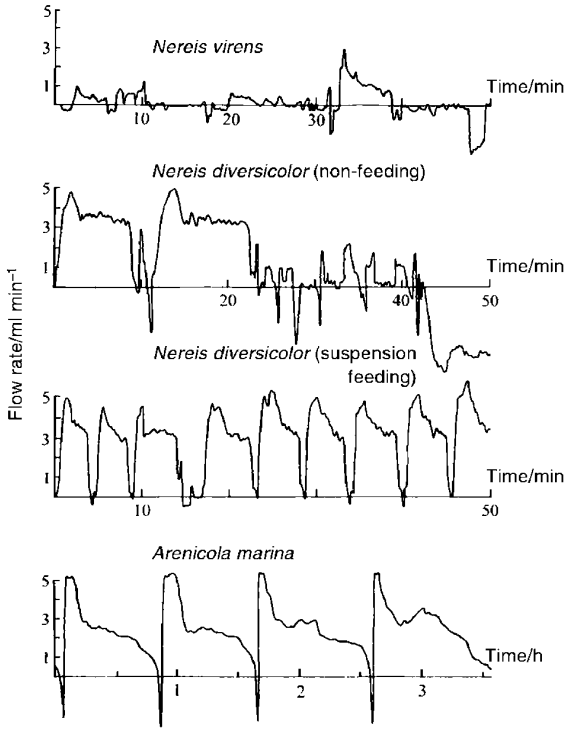

Fig. 6 Irrigation patterns of *Nereis virens*, *N. diversicolor* (under non-feeding and suspension feeding conditions) and *Arenicola marina* (modified from Kristensen *et al.*[11]).

Table 1 Examples of irrigation rate of *Nereis virens*, *N. diversicolor* and *Arenicola marina*. Results are presented both as individual rates [(g worm) h^{-1}] and as population rates (m^2 d^{-1}). The abbreviations (ns) and (s) indicate non-suspension-feeding and suspension-feeding *N. diversicolor*.[9,28]

		Irrigation	
Species	Density/ m^{-2}	Individual/ ml g^{-1} h^{-1}	Population/ l m^{-2} d^{-1}
N. virens	600	21–62	60–180
N. diversicolor (ns)	600	200–250	580–720
N. diversicolor (s)	600	450–500	2600–2900
A. marina	50	10–13	120–160

is suspension-feeding.[9] It also has active irrigation periods of 5–10 min duration, but only interrupted by very short periods of inactivity in a very regular pattern. During the inactive periods it ingests the ripe mucus net and spins a new one. Even when there are no food particles in the overlying water and the suspension-feeding activity of *N. diversicolor* ceases, this worm remains active for about 50% of the time. The irrigation activity of *Arenicola marina* proceeds in cycles of 40 to 60 min duration (Fig. 6). These very regular cycles are probably under the control of a pacemaker situated in the nervous system[27,28] and are linked to the feeding and defecation cycles.

The total volume of water pumped by populations of these worms is impressive (Table 1). Particularly, the suspension-feeding *N. diversicolor* is capable of pumping large volumes of water into the sediment. Natural populations (1000–3000 m^{-2}) of this species may pass a volume corresponding to a water column of 3 to 9 m through their burrows each day.[29] Consequently, their burrows are continuously flushed with overlying water resulting in highly oxic and oxidized conditions in burrow water and surrounding sediment (Fig. 7).

Reworking

Macrofaunal reworking affects the stability and composition of coastal marine sediments. Thus, organic matter deposited in the sediment is usually redistributed, *i.e.* from surface to subsurface layers and *vice versa*. However, various burrow-dwelling animals disturb the sediment structure differently depending on their specific life habit and feeding type.[22,30]

The sedentary *A. marina* is a typical head-down 'conveyor-belt' feeder, which stays more or less permanently in its burrow while eating subsurface sediment and defecating at the surface. This is done in a cyclical pattern in phase with the irrigation cycles. Defecation is evident in Fig. 6 as short bursts of negative water flow caused by the backward movement of the worm. The amount of sediment displaced by populations of *A. marina* is quite considerable with the potential of complete turnover of

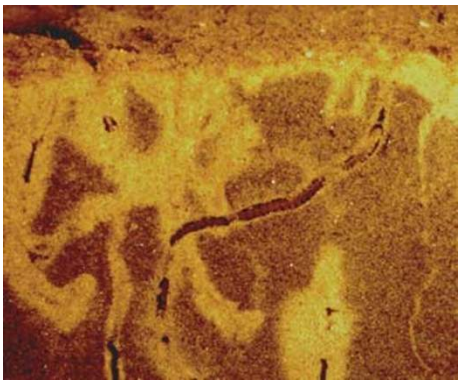

Fig. 7 Cross section of sediment bioturbated by *Nereis diversicolor*. Light patches are oxidized sediment surrounding older burrows. Note that the worm in the centre inhabits a newly constructed burrow without noticeable oxidized sediment.

Table 2 Examples of annual particle reworking rates by *Nereis diversicolor* and *Arenicola marina*. Results are presented both as volume of sediment m^{-2} and as depth of sediment reworked[19,52]

		Reworking	
Species	Density/ ind. m^{-2}	Volume/ $l\,m^{-2}\,y^{-1}$	Depth/ $cm\,y^{-1}$
N. diversicolor	1000	7	0.7
A. marina	40–80	170–400	17–40

up to a 40 cm thick sediment layer per year (Table 2). Since lugworms only ingest particles of less than 2 mm, all larger particles are left behind just below the feeding depth of the worms. Thus, a 'graded bedding'[22] with a distinct layer of gravel and bivalve shells at a depth of about 40 cm can usually be observed in areas with dense populations of *A. marina*. Another visual evidence of the intense reworking by lugworms is the characteristic troughs and piles at the sediment surface indicating the position of feeding funnels and the tail shafts, respectively (Fig. 5).

Free-living polychaetes, like *Nereis* spp., are actively moving around at the sediment surface or within their burrow systems in search for food. Occasionally they abandon burrows, either willingly or forced by inter- and intraspecific fights, and move some distance before digging a new 'home'. The amount of particles moved by these feeding and digging activities of *Nereis* spp. is quantitatively small (*i.e.* 2%) compared with *A. marina* (Table 2). However, the selective feeding of *Nereis* spp. on fresh plants, animals and microorganisms at the sediment surface associated with suspension feeding, subsurface defecation and mucus secretions along burrow walls may redistribute significant amounts of reactive organic matter within the sediment.[9]

Carbon diagenesis

Organic matter is degraded (mineralized) in sediments by an array of aerobic and anaerobic microbial processes with a concurrent release of inorganic nutrients. The rates of decay depend on a variety of factors such as, organic matter quality (*i.e.*, the content of protein, cellulose, lignin, *etc.*), age (decomposition stage) and temperature (season).[31] The chemical composition of organic matter can be generalized according to: $(CH_2O)_x(NH_3)_y(H_3PO_4)_z$, where x, y and z vary depending on the origin and age of the material. For marine organic matter (*e.g.* phytoplankton) having the Redfield composition the stoichiometry is as follows: $x = 106$, $y = 16$, and $z = 1$.

Almost all heterotrophic organisms with aerobic metabolism have the enzymatic capacity to perform a total oxidation of organic carbon. Organic matter may therefore be completely metabolized by a single organism to H_2O, CO_2 and inorganic nutrients using oxygen as electron acceptor according to eqn. (1):

$$(CH_2O)_x(NH_3)_y(H_3PO_4)_z + xO_2 \rightarrow xCO_2 + yNH_3 + zH_3PO_4 + xH_2O \quad (1)$$

However, due to an efficient energy metabolism, a large fraction of the metabolized organic matter ends up as cell material. Aerobic decomposition is unique in the sense that oxygen-containing radicals such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (·OH) are readily formed and consumed. These are capable of breaking strong chemical bonds and thus depolymerize relatively refractory organic compounds rich in aromatic structures like lignin.[32]

As the oxic (oxygen containing) zone in coastal sediments usually is limited to an uppermost mm thick layer, much of

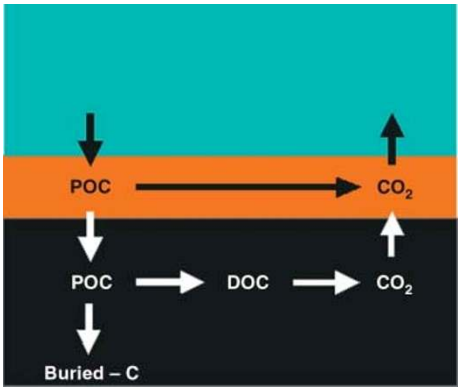

Fig. 8 Simplified carbon cycle in sediment. Particulate organic carbon (POC) is delivered from the water column (blue) to the oxic sediment (orange) where part of it is oxidized to CO_2 by aerobic heterotrophs. Part of the POC is further buried undegraded into anoxic sediment (black) where most of it is converted to dissolved organic carbon (DOC) by hydrolysing and fermenting bacteria. The produced DOC is then oxidized to CO_2 by anaerobic respirers. A small fraction of POC is buried permanently in the sediment and CO_2 is ultimately transported from the sediment to the overlying water by molecular diffusion.

deposited organic carbon is buried in a more or less degraded form into anoxic layers (Fig. 8). Here mutualistic consortia of bacteria accomplish anaerobic decomposition because no single type of anaerobic bacterium seems capable of complete mineralization.[31] Anaerobic bacteria also appear more limited than aerobic organisms in their ability to depolymerize certain large complex molecules. These include among others saturated hydrocarbons,[33] certain pigments[34] and lignin.[35]

Anaerobic decomposition occurs stepwise, involving several different functional types of bacteria. First, large and normally complex polymeric organic molecules are stepwise split into water-soluble monomers (amino acids, monosaccharides and fatty acids) by hydrolysis and fermentation under the production of energy and release of inorganic nutrients,[36] *e.g.* mixed propionate and acetate formation (eqn. (2)):

$$6(CH_2O)_x(NH_3)_y(H_3PO_4)_z \rightarrow xCH_3CH_2COOH + xCH_3COOH + xCO_2 + xH_2 + 6yNH_3 + 6zH_3PO_4 \quad (2)$$

These small organic acids are then oxidized completely to H_2O and CO_2 by a number of respiring microorganisms using a variety of oxidized inorganic compounds as electron acceptors.

The individual anaerobic respiration processes generally occur in a sequence with depth in the sediment according to the availability of electron acceptors: Mn^{4+}, NO_3^-, Fe^{3+}, SO_4^{2-} and CO_2 respiration. The actual sequence is determined by the ability of each electron acceptor to receive electrons, and thus the energy output per degraded organic carbon atom,[31] *e.g.* manganese respiration is energetically more favourable than sulfate reduction. The suboxic zone contains the most potent anaerobic electron acceptors, Mn^{4+}, NO_3^-, and Fe^{3+}. The transition from one electron acceptor to the other downwards in the sediment occurs when the most favourable is exhausted, although some vertical overlap may occur. Two representative examples of anaerobic degradation stoichiometries are manganese and sulfate reduction (eqn. (3) and (4)):

$$CH_3COOH + 4MnO_2 + 8H^+ \rightarrow 4Mn^{2+} + 2CO_2 + 6H_2O \quad (3)$$

$$CH_3COOH + SO_4^{2-} \rightarrow 2CO_2 + S^{2-} + 2H_2O \quad (4)$$

A significant portion of sediment oxygen uptake is not caused by aerobic respiration, but is rather due to reoxidation of reduced inorganic metabolites (*e.g.*, NH_4^+, Mn^{2+}, Fe^{2+}

and H_2S) close to the oxic/anoxic interface. Thus, up to 85% of the sulfide produced by sulfate reduction is not trapped permanently by reactions with iron and other metals, but is continuously diffusing upwards to be reoxidized in the near-surface sediment.[37] About 50% or more of the total sediment oxygen uptake is usually consumed directly or indirectly by oxidation of sulfide.[38] Reoxidation can be a pure chemical process, but it is usually mediated by chemoautotrophic microorganisms.

The strict vertical distribution of electron acceptors, as mentioned above, is an over-simplification of the true spatial distribution. The influence of sediment inhomogeneities, such as worm burrows, on porewater profiles and vertical distribution of microbial processes has been clearly documented.[22] Furthermore, patches associated with, *e.g.*, faecal pellets may create anaerobic microniches, where anaerobic processes, such as denitrification and sulfate reduction, occur in otherwise oxic surface sediments.[39,40]

Nevertheless, the usually observed decreasing degradation rate with depth in sediments is not solely caused by the less efficient electron acceptors in the deeper layers, but rather by decreasing degradability of organic matter.[32]

Carbon oxidation in sediment inhabited by *Nereis* spp. and *Arenicola marina*

Impact on microbial reaction rates

The first studies examining the importance of *Nereis* spp. and *Arenicola marina* on sediment processes focused on the role of these animals for sediment–water fluxes and vertical porewater profiles of various solutes.[41–43] These studies were supplemented with measurements of *e.g.* burrow architecture and defecation rates.[12,19] More recent biogeochemical studies employing a variety of experimental and modelling techniques have gained important new knowledge on the mechanisms controlling reaction rates in bioturbated sediments in general[23,44] and more specifically in nearshore sediments affected by *Nereis* spp. and *Arenicola marina*.[9,45,46]

Fluxes. Irrigation is particularly important in enhancing solute exchange between overlying water and pore fluids.[22] However, it is not an easy task to measure the impact of infauna on solute fluxes in nature due to the obvious lack of fauna-free sediment patches comparable to bioturbated locations. Sieving and homogenizing sediment to remove fauna and other inhomogeneities have partly solved this problem. Measurements are then done in laboratory microcosms by reintroducing known densities of animals, while defaunated controls are kept as a reference.[42] Despite its inherent limitations (see later), this technique has been and still is widely used for certain purposes.[9,45] Other studies use intact sediment microcosms, which are deoxygenated by N_2 flushing in order to force the existing fauna out of the sediment followed by introduction of known densities of selected species when aeration is resumed.[47] Unfortunately, only few studies have made comparable *in situ* measurements without manipulations, and few or none have yet been published for *Nereis* spp. and *Arenicola marina*.

Although the above-mentioned manipulative techniques are problematic, they have provided valuable information on the potential impact of burrow dwelling worms on total sediment metabolism. It has been shown that *Nereis* spp. stimulates benthic metabolism in manipulated sediment, measured as O_2 uptake or CO_2 production, by 45 to 179% compared with defaunated sediments (Table 3). Furthermore, in a study where homogenized sediment microcosms with *Nereis virens* ($600\ m^{-2}$) were combined with flowmeter measurements on individual worm + burrow systems, Kristensen[42] found that the diffusive flux across burrow walls accounted for 31% of the total oxygen uptake, while only 11% was consumed by *Nereis virens* itself. Diffusive flux across the sediment/water interface accounted for the remaining 58% of the oxygen uptake.

Table 3 Enhancement of benthic metabolism (O_2 uptake or CO_2 release) in sandy sediment inhabited by *Nereis* spp. and *Arenicola marina*. Values are given as percent difference between faunated and defaunated sediment (flux enhancement). The experimental conditions are indicated as: homog. = homogenized sediment in laboratory, intact = intact, but defaunated sediment in laboratory, *in situ* = *in situ* measurements[a]

Species	Exp. conditions	Density/ ind. m^{-2}	Flux enhancement (%)
N. virens[42]	homog.	600	74
N. virens[54]	homog.	1800	152
N. virens[47]	intact	800	79
N. virens[9]	homog.	600	74
N. diversicolor[48]	intact	1990	70
N. diversicolor[49]	homog.	1430	45
N. diversicolor[50]	intact	1390	81
N. diversicolor[50]	*in situ*	1000	25
N. diversicolor[46]	homog.	1190	174
N. diversicolor[45]	homog.	600	81
N. diversicolor[9]	homog.	600	94
N. diversicolor[51]	intact	2000	98
A. marina[45]	homog.	600	260
A. marina[52]	*in situ*	60	10
A. marina[52]	homog.	200	162

[a]Note that specimens of *A. marina* used in homogenized sediment were juveniles.

Only few attempts have been made to determine the flux enhancement by *A. marina* under manipulated laboratory conditions. The few data available indicate that this species have a higher capacity to increase fluxes than *Nereis* spp. Upward percolation of irrigated water through the feeding funnel forces porewater rich in solutes out of the sediment, which is more efficient than the combined action of radial diffusion into the burrow and advective transport out of the burrow as in the *Nereis* case.[54]

The faunal induced flux enhancement reported from manipulated non-steady laboratory systems are not comparable to *in situ* conditions as evidenced from the much lower (10 and 25%, Table 3) enhancement by *Arenicola marina* and *Nereis diversicolor* under natural conditions.[46,52] The degree of flux stimulation by benthic infauna is therefore highly dependent on the type of sediment manipulation made, and the measured flux enhancement does not always reflect true changes in microbial activity.[54] A significant part of fluxes is rather caused by porewater flushing, *i.e.* removal of porewater CO_2 or sulfide (reducing equivalents with subsequent reoxidation at the surface) *via* infaunal irrigation. This is particularly true in experiments using homogenized or otherwise defaunated sediment, where animals are added several days after the establishment of sediment microcosms. CO_2 or reducing equivalents produced by microbial metabolism within the sediment during such long conditioning period tends to accumulate in the porewater. Immediately after addition of infauna such as *Nereis* spp, these porewater solutes are rapidly transported into the newly established burrows and carried to the overlying water by the irrigation current. A recent study has shown that the transport of porewater solutes into burrows is dominated by radial diffusion in impermeable fine-grained silty sediments, while porewater advection is more important in permeable sandy sediments.[53] As a consequence, the flux is extremely high initially and first approaches steady state gradually after a time period of typically 1–2 weeks[47] (Fig. 9). The removal of dissolved metabolites from the porewater is clearly evident as significantly lowered concentrations when vertical profiles of *e.g.* CO_2 in bioturbated sediment are compared with defaunated sediment (Fig. 10).

Organic matter replenishment is another problem with the

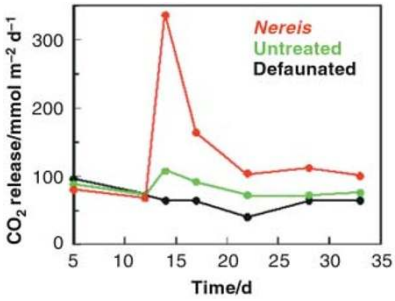

Fig. 9 Release of CO_2 from sediment microcosms. Intact sediment cores were either kept untreated (green) or defaunated on day 6 by deoxygenation (N_2 purging). Defaunated cores were either kept without animals (black) or added *Nereis diversicolor* at a density of 1390 m^{-2} on day 13 (after Hansen and Kristensen[46]).

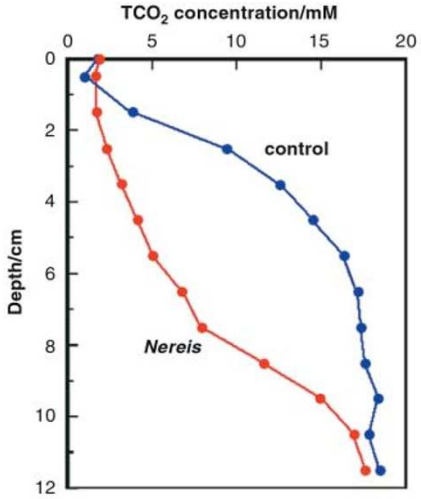

Fig. 10 Porewater profiles of TCO_2 in sandy sediment inhabited by 600 *Nereis diversicolor* m^{-2} (*Nereis*) or defaunated (control) (after Kristensen and Hansen[53]).

manipulated laboratory experiments. The microcosms are rarely continuously supplied with new organic substrates to balance the removal by decomposition. Even the supply from benthic diatoms may be impaired as the experiments usually are performed in darkness. As a consequence, true steady state will never be reached. The stable flux conditions usually observed after the initial porewater flushing (Fig. 9) can therefore only be considered a short-term pseudo steady state. In due course (months), fluxes must decrease to very low levels, and eventually be lower in bioturbated than defaunated sediment due to exhaustion of reactive organic matter.

Decomposition rates. The flux enhancement reached in manipulated systems, when the pseudo steady state is approached immediately after the initial porewater flushing, should be considered a measure of the enhanced metabolic capacity of all heterotrophic organisms in the sediment.[55] However, this proposition is difficult to test experimentally under natural conditions because defaunated sediments underlying oxic water columns are rare. An alternative approach is to apply a speculative scenario based on the current knowledge on effects of *Nereis* spp. and *Arenicola marina*.

The frame of scenario is a hypothetical marine sediment environment, with no temporal (seasonal and diurnal) variability, which is supplied continuously with organic carbon from above by deposition on the surface. The environment consists of two previously fauna-free, but adjoining sites: To one site a population of *Arenicola marina* is introduced whereas the other remains defaunated. They both receive the same quantity and

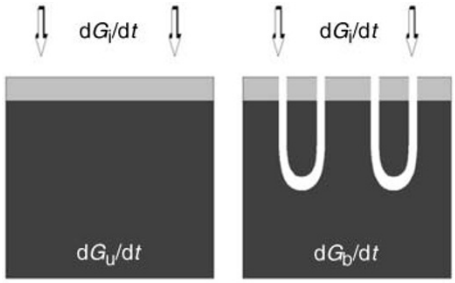

Fig. 11 A hypothetical marine sediment with two adjoining sites. *Left*: defaunated. *Right*: with a normal density of *Arenicola marina*. Arrows indicate sedimentation of reactive organic matter at a rate of dG_i/dt. Bulk sediment organic matter decomposition is dG_u/dt at the defaunated site and dG_b/dt at the faunated site (after Kristensen[55]).

quality of organic input (dG_i/dt) (Fig. 11). Thus, the deposit-feeding *A. marina* is not assumed to increase organic carbon deposition (see later). The bulk decomposition rate within the sediment is assumed to be first-order with respect to the reactive organic carbon content: $dG/dt = k\ G$, where k is the first-order decomposition coefficient (decomposition capacity) and G is the inventory of reactive organic carbon.[56] *A. marina* is assumed to enhance the capacity for organic matter decomposition, and thus to increase the decomposition coefficient compared with the defaunated sediment, *i.e.* $k_b > k_u$. Initially (just after introduction of *A. marina*), the total metabolism of the faunated ($dG_b/dt = k_b G_u$) system is k_b/k_u times higher than that of the defaunated system ($dG_u/dt = k_u G_u$) because the reactive organic inventory G_u is similar in both systems. In this situation, the enhanced decomposition due to *A. marina* is independent of the organic input, and simulates the above mentioned manipulated laboratory experiments when the initial porewater flushing has ceased. Hence, in their manipulated system, Kristensen and Blackburn[54] found that the enhanced decomposition capacity (k_b/k_u, based on measured disappearance of particulate organic carbon) of 2.6 in the presence of *Nereis virens* actually was similar to the enhanced oxygen uptake (factor 2.5) just after the initial flushing period.

However, the present model approach (Fig. 11) predicts that the amount of organic carbon mineralization at steady state must be equivalent to that being supplied (ignoring permanent burial), irrespective of the presence of *A. marina*: $dG_b/dt = dG_u/dt = dG_i/dt$. The steady state pool of reactive organic carbon in the faunated sediment must then be lower than in the defaunated sediment in proportion to the ratio between decomposition coefficients: $G_b = k_u/k_b\ G_u$. Basically, the difference between the two systems is an increased decomposition capacity (*i.e.* the decomposition coefficient, k) in the faunated system and thus a decreased total pool of reactive organic carbon at steady state compared with a defaunated system (Fig. 12), while the bulk decomposition rate and flux are similar at both sites (see *A. marina* under *in situ* conditions in Table 3).

Decomposition must be increased when the faunal activities enhance deposition of organic matter to the sediment, whereas the organic pool may reach a level higher than, similar to or lower than in the defaunated sediment, depending on the functional type, density and size of animals present. In a very illustrative experiment, Christensen *et al.*[9] examined the impact of suspension-feeding *N. diversicolor* and non-suspension-feeding *N. virens* on carbon dynamics in organic-poor sediment when exposed to phytoplankton in the overlying water. The presence of phytoplankton resulted in a 30-fold higher deposition (clearance, Fig. 13) of particulate carbon to the sediment inhabited by *N. diversicolor* than to *N. virens* and defaunated sediment. Concurrently, oxygen uptake was increased by a factor of 3 in sediment with *N. diversicolor*, but only a factor of about 1.5 in *N. virens* and defaunated sediment (Fig. 14).

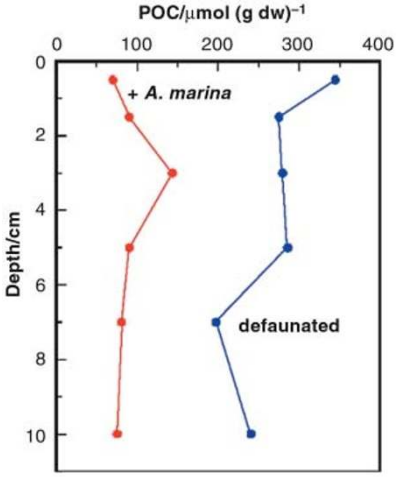

Fig. 12 Vertical profiles of POC content in two adjacent sandy sediment sites (5 m apart) from Løgstør Broad, Denmark. The + *A. marina* site was inhabited by a population of *A. marina* at a density of 60 m^{-2}. The defaunated site contained no *A. marina* (modified from Kristensen *et al.*[11]).

About 30% of the deposited carbon in the *N. diversicolor* sediment was oxidized and lost rapidly as excess CO_2 flux to the water column. Incorporation into *N. diversicolor* tissues accounted for 45% of the carbon, while the remaining accumulated within the sediment. In the *N. virens* sediment, where no excess phytoplankton deposition occurred, decomposition resulted in a net loss of sedimentary carbon due to the enhancement of microbial decomposition by *N. virens*. Thus, two almost identical species may either enrich or impoverish the organic inventory of sediments depending on their life habit.

The intense reworking activity of conveyor-belt feeders like *Arenicola marina* results in subduction of surface sediment at rates significantly higher than natural sedimentation rates. As a consequence, benthic microalgae and other labile or digestible organic particles (*e.g.* bacteria) are drawn into subsurface layers of the sediment. Thus, Retraubun *et al.*[57] observed similar concentrations of benthic diatoms in the feeding funnel and feeding pocket of *A. marina* than at the sediment surface. These reactive organic substrates not only serve as nutrition for the worms, but also displace microbial decomposition within the sediment. The typical exponential decrease in anaerobic carbon oxidation with depth in sediments affected by passive sedimentation is replaced by lower surface rates and only gradually decreasing rates with depth within the bioturbated depth of intensively reworked sediments (Fig. 15). The total rate of microbial activity integrated within the bioturbated depth may not change significantly by the displacement of organic matter and microbial processes. However, the trough

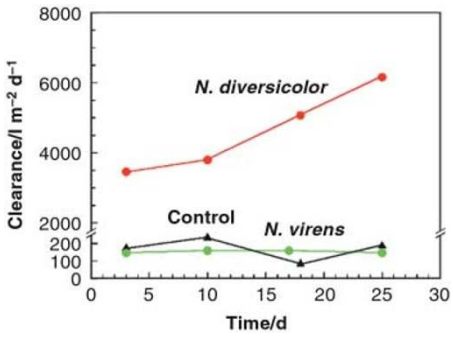

Fig. 13 Clearance (water volume cleared of algae) in microcosms supplied with 10 000 cells ml^{-1} of *Rhodomonas* sp. in the overlying water throughout a 27 day experimental period (modified from Christensen *et al.*[9]).

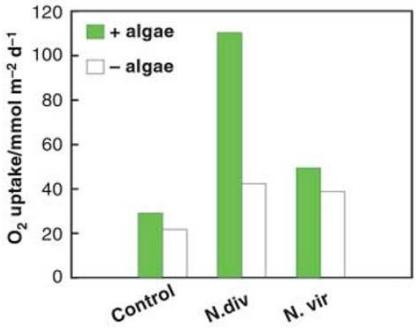

Fig. 14 Oxygen uptake in microcosm with and without addition of *Rhodomonas* sp. in the overlying water (modified from Christensen *et al.*[9]).

frequently created by the feeding funnel of *A. marina* may act as a subduction trap for detritus swept horizontally along the sediment surface by currents and waves,[43] and thus enhance both the inventory of organic substrates as well as the total depth integrated benthic metabolism. Under these circumstances, the crude assumptions and the general conclusions made in the model for *A. marina* discussed above do not hold. Anyway, the model still provides a basic understanding of the balance between reaction rates and the inventory of reactive organic matter in sediments affected by burrowing fauna.

Causes for stimulated microbial decomposition

A number of macrofaunal activities are known or have been inferred to cause the enhancement of microbial metabolism and capacity for organic matter degradation in bioturbated sediments:[23] particle manipulation, grazing, excretion/secretion, burrow/tube construction, irrigation and particle reworking. The two latter activities, which are the focus of this paper, are considered particularly important controlling factors for carbon diagenesis in *Nereis* spp. and *Arenicola marina* inhabited sediments.[4,55]

The current knowledge on the underlying mechanisms for the impact of irrigation (defined here as downward transport of oxidants and upward transport of metabolites in sediments) and particle reworking (defined here as transfer of organic matter and redox sensitive minerals between redox zones) by species like *Nereis* spp. and *A. marina* on carbon diagenesis in coastal sediments will be summarized in the following. While acknowledging the simultaneous and inseparable nature of these activities, they will be treated individually and compared within and between species, when possible.

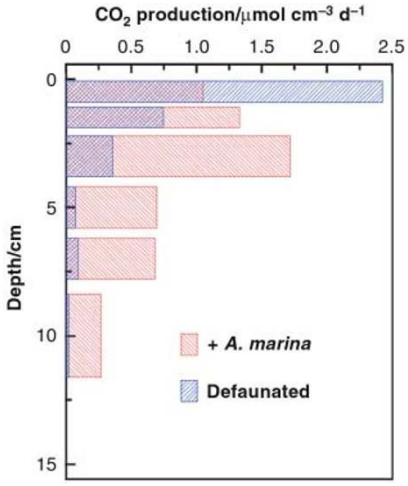

Fig. 15 Vertical profiles of anaerobic carbon oxidation in defaunated and *Arenicola marina inhabited* sandy sediment (modified from Kristensen *et al.*[11]).

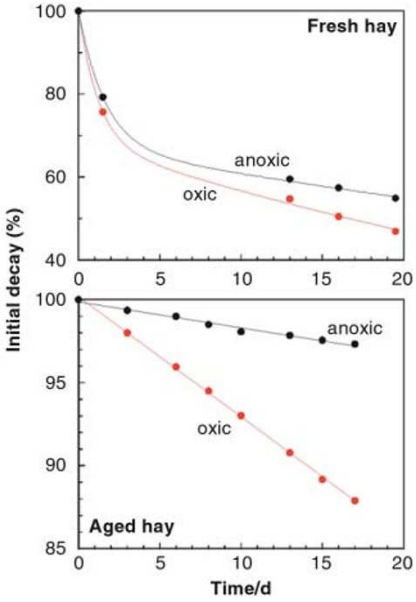

Fig. 16 Decay pattern of fresh barley hay (upper panel) and 50 days predecomposed (aged) barley hay (lower panel) in oxic and anoxic marine sediment (modified from Kristensen and Holmer[59]).

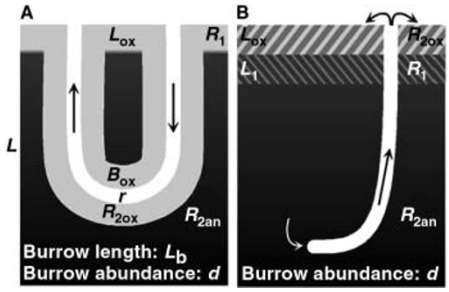

Fig. 17 A schematic presentation of the volumetric model used for quantification of carbon reaction rates in sandy coastal sediment with a depth of L cm: A, with irrigated burrows of the polychaetes *Nereis diversicolor*. The grey zones indicate oxic surface sediment (thickness L_{ox} cm) and oxic burrow walls (thickness B_{ox} cm). All burrows have a radius of r cm and a length of L_b cm. B; with reworking by the head-down conveyor-belt feeding polychaetes *Arenicola marina*. The lightly hatched zone (L_{ox}) indicates the oxic surface sediment. The darkly hatched zone (L_1) indicates surface related labile material displaced into anoxic sediment. In both cases, the carbon oxidation rate (R_1) of the labile detritus under both oxic and anoxic conditions is A_1 times faster than the carbon oxidation rate (R_{2an}) of the partly degraded detritus in the anoxic black sediment ($R_1 = A_1\ R_{2an}$). When deep subsurface sediment is exposed to oxygen in irrigated burrows or by reworking the reaction rate is enhanced A_2 fold ($R_{2ox} = A_2\ R_{2an}$) (modified from Kristensen and Holmer[59]).

The role of oxygen. A number of studies have emphasized that aerobic and anaerobic decomposition are comparable for fresh and reactive organic substrates, while aerobic processes proceed much faster for partly degraded and refractory compounds.[34,58,59] In an experiment where carbon mineralization of ^{14}C labelled fresh and aged diatoms (*Skeletonema costatum*) and barley hay (*Hordeum vulgare*) was followed for about one month, Kristensen and Holmer[59] showed that the initial decay of fresh materials occurs at almost the same rate in both oxic and anoxic sediment (Fig. 16). After ageing, degradation is 5 to 10 times faster under oxic than anoxic conditions. Based on these and similar results it has been argued that introduction of oxygen into anoxic sediment by macrofaunal irrigation or translocation of organic matter from anoxic to oxic environments by particle reworking promotes decomposition of organic matter in sediments.[44,59]

Quantitative estimates of the enhanced decomposition caused by injection of oxygen into actively irrigated burrows or by oxygen exposure due to particle reworking are rare.[55] By the use of a modified version of the simple volumetric model presented by Kristensen and Holmer,[59] rough estimates can be provided for the stimulated carbon reaction rate in sandy coastal sediment shortly after the introduction of macrobiotic activity in the form of either irrigated burrows of *e.g. Nereis diversicolor* or burrows reworked by *e.g. Arenicola marina*.

In both cases, the calculations are based on the following common assumptions: (i) all diagenetic processes occur in the upper L cm of the sediment column; (ii) the oxic surface zone is L_{ox} cm thick; (iii) the rate of deposition (*e.g.* phytoplankton) or production (*e.g.* benthic diatoms) at the sediment surface of labile organic matter is similar irrespective of the species present; (iv) the fresh and labile detritus is mineralized A_1 times faster (both in the presence and absence of oxygen) than the old and partly degraded detritus in the anoxic zone ($R_{1ox} = R_{1an} = R_1 = A_1\ R_{2an}$); (v) mineralization of old and partly degraded organic matter from anoxic zones is enhanced by a factor of A_2 when exposed to oxygen at the surface during reworking or along irrigated burrow walls ($R_{2ox} = A_2\ R_{2an}$); (vi) no depth dependent change in degradability of sediment detritus occurs in oxic and anoxic zones ($dR/dx = 0$), and the anoxic mineralization rate is independent of electron acceptors.

In the *Nereis diversicolor* irrigation model (Fig. 17(a)) the following specific conditions are assumed: (i) all fresh and labile detritus deposited at the surface is located in the oxic surface layer; (ii) the *N. diversicolor* abundance is d individuals m^{-2}; (iii) burrows are U-shaped with two openings at the surface and a total length of L_b cm and a radius of r cm; (iv) irrigation is continuous and the oxic zone around burrows is permanently B_{ox} cm thick. By relating volumes with reaction rates in the various zones, total sediment carbon oxidation m^{-2} in the presence and absence of irrigated burrows with oxic walls can be estimated according to eqn. (5) (irrigated) and (6) (defaunated):

$$C_{iox} = R_{2an}\,(V - (V_{ox} + V_{ban} + V_{wox})) + R_1\,(V_{ox} - V_{box}) + R_{2ox}\,V_{wox} \quad (5)$$

$$C_{dox} = R_{2an}\,(V - V_{ox}) + R_1\,V_{ox} \quad (6)$$

where: $V = L \times 10^4$ is total sediment volume ($cm^3\ m^{-2}$) to depth L; $V_{ox} = L_{ox} \times 10^4$ is volume oxic surface sediment without burrows; $V_{ban} = \pi\ r^2\ (L_b - 2L_{ox})\ d$ is subsurface burrow lumen volume; $V_{box} = \pi\ r^2\ 2L_{ox}\ d$ is surface burrow lumen volume; $V_{wox} = \pi\,(B_{ox}^2 + 2r\ B_{ox})\,(L_b - 2L_{ox})\ d$ is oxic subsurface burrow wall volume. The initial enhancement of carbon oxidation caused by the presence of irrigated burrows with oxic walls is then, $E_i = C_{iox}/C_{dox}$.

In the reworking case with *Arenicola marina* (Fig. 17(b)) the following specific conditions are assumed: (i) reworking is continuous and subsurface sediment is distributed in an even layer on top of the sediment with a steady state thickness at least similar to the depth of the oxic surface layer (L_{ox}); (ii) labile surface sediment with a thickness similar to that in the defaunated situation ($L_l = L_{ox}$) is continuously pushed downward into the anoxic zone; (iii) the *A. marina* abundance is d individuals m^{-2}; (iv) since burrows are assumed vertical and the presence of oxic subsurface sediment (*e.g.* burrow walls) is ignored, the burrow lumen can be excluded from calculations (these assumptions are clearly false, but necessary, when only reworking activities are considered). From sediment volumes and reaction rates in the various zones, total sediment carbon oxidation (m^{-2}) in the presence and absence of sediment reworking can be estimated according to eqn. (7) (reworked) and (8) (defaunated), where the volume of reduced subsurface

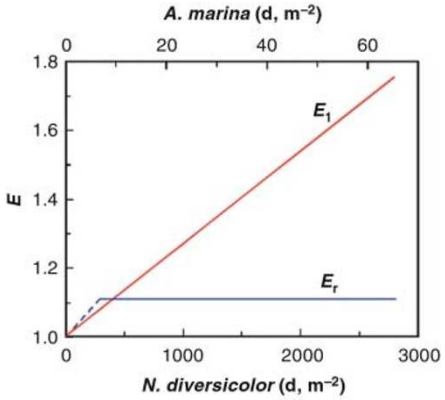

Fig. 18 Enhancement of total sediment carbon oxidation due to increased microbial degradation in the presence of irrigated burrows ($E_1 = C_{iox}/C_{dox}$) and reworking ($E_r = C_{rox}/C_{dox}$) as a function of abundance of *Nereis diversicolor* and *Arenicola marina*. Other variables are fixed: $L = 20$ cm, $L_b = 20$ cm, $L_{ox} = 0.3$ cm, $r = 0.3$ cm, $B_{ox} = 0.2$ cm, $A_1 = 20$ and $A_2 = 10$. See text for further details (modified from Kristensen and Holmer[59]).

sediment deposited at the oxic surface (V_{rox}) is similar to the volume of buried sediment containing labile detritus (V_l).

$$C_{rox} = R_{2an}\,(V - (V_l + V_{rox})) + R_1\,V_l + R_{2ox}\,V_{rox} \quad (7)$$

$$C_{dox} = R_{2an}\,(V - V_{ox}) + R_1\,V_{ox} \quad (8)$$

where: $V = L \times 10^4$ is total sediment volume ($cm^3\,m^{-2}$) to depth L; $V_{ox} = L_{ox} \times 10^4$ is volume oxic surface sediment without burrows; $V_l = L_l \times 10^4\,cm^3\,m^{-2}$ is volume of buried sediment containing labile detritus; $V_{rox} = L_{ox} \times 10^4\,cm^3\,m^{-2}$ is volume of reduced subsurface sediment deposited at the oxic surface. However, due to the continuous input of labile detritus and deposition by reworking a dilution of the labile material into a larger sediment volume obviously occurs. Nevertheless, based on the assumption above, the volumetric reaction rate should remain unaffected. The initial enhancement of carbon oxidation caused by sediment reworking are then, $E_r = C_{rox}/C_{dox} = (L + (A_1 + A_2 - 2)\,L_{ox})/(L + ((A_1 - 1)\,L_{ox})$.

In the irrigation model (eqn. (5) and (6)), the variables L, L_b, L_{ox}, r, B_{ox}, A_1 and A_2 may all change depending on factors like season, sediment type and worm size. However, for simplicity we have chosen to keep them all constant: $L = 20$ cm; $L_b = 20$ cm; $L_{ox} = 0.3$ cm; $r = 0.3$ cm; $B_{ox} = 0.2$ cm; $A_1 = 20$; $A_2 = 10$. These fixed values are chosen based on past and present experience on nereid polychaetes[10,60] and sediment biogeochemistry in shallow sandy areas.[61] By varying d, our model predicts that the degree of stimulation is directly proportional to worm abundance, when the oxic zone around burrows is assumed independent of the distance between burrows (Fig. 18). Accordingly, the enhancement of total sediment carbon oxidation due to 2000 irrigated burrows of *N. diversicolor* (m^{-2}) is estimated to $E_i = 1.61$. This is within the previously mentioned range of published enhancements of benthic metabolism caused by a similar abundance of these animals. However, as the worm abundance increases, the anoxic to oxic volume of subsurface sediment and thus the production and reoxidation of reduced metabolites decrease. The oxic zone around burrows may therefore expand, resulting in a proportionally larger oxic volume at high abundances, and thus larger impact of irrigated burrows on sediment decomposition. The upper limit is reached at hypothetically high abundances when all subsurface sediment is converted to oxic burrow walls.

The reworking model (eqn. (7) and (8)) predicts that carbon oxidation in the presence of *A. marina* is enhanced by $E_r = 1.11$, when the variables, L, L_{ox}, A_1 and A_2 are similar to those used in the irrigation model, and that the enhancement is independent of worm abundance, d (Fig. 18). This prediction is only valid when reworked subsurface sediment containing reactive organic material covers the sediment surface to a depth similar to the oxic zone and that reaction rates are not so fast as to eliminate entirely the organic material exposed in a single transit. This means that below a certain threshold the enhancement must be proportional to abundance. As one average sized individual deposits $1.4 \times 10^{-3}\,cm\,d^{-1}$ sediment at the surface,[19] a population size of $7\,m^{-2}$ is needed to deposit a 0.3 cm layer (equivalent to L_{ox}) every month. The actual threshold of abundance is probably lower than this limit, since there were no signs of changes in reactivity of aged materials exposed to oxygen for one month.[60]

It is important to note that these model calculations are only valid for the initial conditions after introduction of macrobenthic activity. For a fixed influx of material, the steady state mass of reactive organic matter in a sediment deposit where decomposition rates are enhanced by faunal activities must be lower than for a defaunated situation (see the "Decomposition rates" sub—section above). Nevertheless, these model examples clearly illustrates that decomposition capacity of partly degraded organic matter along oxic walls of irrigated infaunal burrows is enhanced progressively more than by exposure of subsurface sediment to oxygen during reworking.

In the reworking case, where *A. marina* is used as model organism, oxygen effects due to irrigation of this worm are ignored. As mentioned earlier, the burrow structure and irrigation type of *A. marina* may result in comparable or larger impact on sedimentary reaction rates than that of *N. diversicolor*, and should be recognized and included in sedimentary budget predictions. As a consequence, the overall impact (including both reworking and irrigation) of *A. marina* may very well be higher than of *N. diversicolor*. Accordingly, Banta *et al.*[45] reported up to 3-fold higher stimulation of carbon oxidation by *A. marina* than *N. diversicolor*.

The oxygen effect of bioturbation on reaction rates in sediments may be masked by other, and in this context, less known factors. Recently, Mikkelsen and Kristensen[62] conducted an experiment, where fresh and aged (after 55 day aerobic decay) ^{14}C labelled *fucus serratus* detritus was placed at the oxic surface or buried into anoxic subsurface layers of *N. diversicolor* bioturbated and defaunated sediment. According to the propositions made above, it was expected that degradation of fresh detritus would proceed at similar rates irrespective of its position within the sediment and the presence of *N. diversicolor*. Degradation of aged detritus, on the other hand, should be strongly stimulated by irrigation activities of *N. diversicolor* when buried into anoxic sediment. The results showed, as expected, that the carbon mineralization of refractory detritus buried in anoxic sediment only proceeded at 28% of the rate of detritus deposited at the oxic surface (Fig. 19). It was surprising, though, that mineralization of

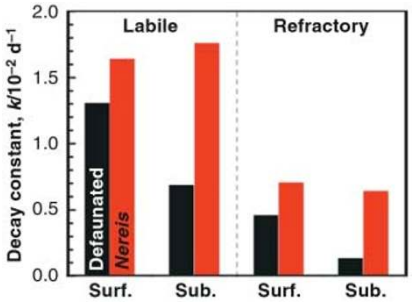

Fig. 19 Decay constants (k) for the mineralization of ^{14}C labelled *Fucus serratus* detritus. Labile and refractory detritus were deposited at the surface (Surf.) and in subsurface (Sub.) sediment of defaunated and *Nereis diversicolor* bioturbated microcosms held at 15 °C (Mikkelsen and Kristensen[62]).

labile detritus was reduced to half (53%) when buried in anoxic sediment. The presence of *N. diversicolor* always enhanced carbon mineralization of added detritus. The effect was modest for surface-deposited detritus (25–54%) and was probably caused by feeding, assimilation and respiration by the worms. Mineralization of subsurface-deposited detritus was increased dramatically (155% for labile detritus and 392% for refractory detritus), reaching a level comparable to the corresponding treatments with surface-deposited detritus. The more than two-fold difference in stimulation between the two types of detritus must be caused by the stronger oxygen effect on decay of refractory detritus. The unexpected large decrease in mineralization of subsurface-deposited labile detritus and subsequent increase in the presence of *N. diversicolor* must be caused by other factors than oxygen availability. A plausible explanation for this discrepancy may be inhibition of microbial activity by accumulation of noxious metabolites in defaunated subsurface sediments, and subsequent alleviation in the presence of irrigating infauna.[23]

Removal of metabolites. Irrigation not only promotes metabolic processes by supplying electron acceptors, like oxygen, to bioturbated subsurface sediments, but also net reactions in anoxic regions of inhabited sediments are stimulated.[63] This implies that net rates of anaerobic microbial processes are controlled by the exchange of other solutes than oxygen during irrigation. Metabolites, such as CO_2, ammonium and sulfide ions (Fig. 10) in particular, are efficiently removed from sediment porewaters by infaunal irrigation.

It was a puzzle for years to understand why the total CO_2 release from the sediment in defaunated microcosms of different thickness, but containing the same sediment type, was almost independent of sediment thickness. As a consequence, the volume specific net mineralization must be inversely related to sediment thickness (Fig. 20). Recently, Aller and Aller[23] convincingly showed that net mineralization rates increase dramatically as diffusion scale (sediment thickness) decreases and efficiency of solute exchange with overlying water increases. This demonstrates that irrigation of sediment may result in an infaunal density-dependent increase in mineralization, microbial activity and sediment-water solute fluxes of constituents not normally considered sensitive to concentration dependent reactions. The effects are relatively modest (1.5–2.0 times) for diffusion distances larger than 1 cm, but become increasingly important at small scales (Fig. 20). Thus, anaerobic mineralization of organic matter increases with increasing diffusive exchange or, in other words, macrofaunal burrow spacing and irrigation intensity.

The dependence of reaction rates on diffusion scale presumably reflects the balance between competing reactions and processes that vary as a function of concentration of reactants, products, or inhibiting constituents. Aller and Aller[23] considered three possible cases as representative examples

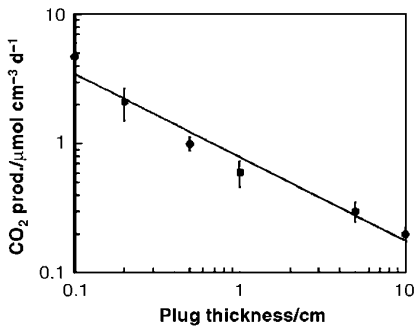

Fig. 20 Volume specific carbon oxidation as a function of diffusion scale (plug thickness). The experiment was conducted under anoxic conditions using sediment plugs of a diameter of 5 cm and a length ranging from 0.1 to 10 cm (Valdemarsen and Kristensen[64]).

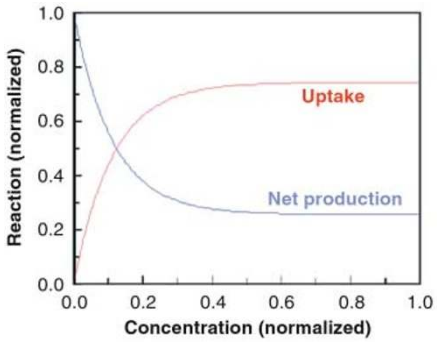

Fig. 21 Balance between production of nutrients by microorganisms and uptake by assimilation or precipitation as a function of concentration (proportional to diffusion scale). Reaction is normalized to the maximum production rate and concentration is normalized to half saturation (K_m) (modified from Aller and Aller[23]).

capable of explaining the observed reaction rate–diffusion scale patterns: (i) coupled mineralization–biological uptake, where the balance between a constant rate of nutrient mineralization and a concentration dependent (Michaelis–Menten kinetics) assimilation favours a high net mineralization at small diffusion scales (Fig. 21); (ii) coupled mineralization–abiogenic precipitation, where assimilation from case (i) is substituted with concentration dependent precipitation reactions. Thus progressively higher removal of solutes (*e.g.* CO_2) is due to precipitation (*e.g.* carbonates) when the diffusion scales become larger; (iii) mineralization–inhibiting metabolite interactions, where the response of mineralization activity to transport scale results from removal of inhibiting metabolites (Fig. 22). As transport scale decreases, the concentration of metabolic products and reaction inhibitors must also decrease, resulting in an overall increase in mineralization rate at a fixed value of biomass. If relaxation of inhibitory effects enhances microbial growth, mineralization may also change as a result of the higher reaction capacity by the increased biomass under more favourable conditions.

The proposed effect of infauna on metabolite dependent processes has not yet been confirmed from direct measurements in bioturbated sediments. However, relaxation of metabolite effects is a very plausible contributing explanation for the observed irrigation effect of *Nereis* spp. and *Arenicola marina* on benthic carbon mineralization.

Future developments

Although the understanding of bioturbation effects in general and by *Nereis* spp. and *Arenicola marina* in particular has advanced considerably within the last couple of decades, the

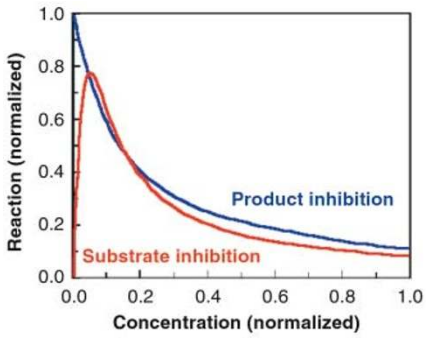

Fig. 22 Idealized example of product and substrate inhibition of microbial reactions as a function of product and substrate concentration. Reaction is normalized to the maximum production rate and concentration is normalized to half inhibition (K_i) (modified from Aller and Aller[23]).

interactions with transport regime (diffusion scale), decomposition pathways (electron acceptor availability), microbial communities (bacterial populations) and associated processes are some of the important areas that remain largely unexplored. Furthermore, there is, as mentioned earlier, an urgent demand for conducting measurements by *in situ* approaches to avoid elucidating artefacts caused by the frequently used manipulative laboratory experiments.

Diffusion scale. The three possible cases suggested by Aller and Aller[23] as explanations for the reaction rate response to changing diffusion scale (1, biological uptake; 2, abiogenic precipitation; and 3, inhibition) must be experimentally verified. The first step must be to determine the response of anaerobic sediment processes to the addition and removal of a variety of potentially inhibiting metabolites, either individually or in chosen combinations. This should be done in anoxic sediment incubations, where solute concentrations in the porewater as well as reaction rates can be controlled and measured simultaneously. In the second step, reaction rates and the concentration of inhibitory metabolites should be measured in sediment microcosms with different densities of selected infaunal species. The third and most critical step will be to confirm that the interactions between reaction rates and inhibitory metabolites, which were revealed in steps one and two, are also active under *in situ* conditions. This task is complicated by the unpredictable seasonal, diurnal and spatial variations in the field and demands a competent small-scale approach conducted over long time series.

Electron acceptor availability. It has been shown, beyond any doubt, that infaunal irrigation increases the availability of oxygen as an electron acceptor in deep sediment strata. As a consequence, the availability of nitrate as electron acceptor for anaerobic respiration (denitrification) also increases due to downward irrigation transport and nitrification occurring in oxic burrow walls.[51,65,66] However, direct evidence for increased availability of Mn^{4+} and Fe^{3+} as electron acceptors in bioturbated sediments is lacking. Based on strong evidence, it has been argued, though, that the large contribution of Mn^{4+} and Fe^{3+} respiration to total benthic metabolism in manganese- and iron-rich deposits is primarily caused by bioturbation (particularly reworking).[67,68] Although visual observations of brownish oxidized zones associated with deep burrow structures (Fig. 7) clearly indicate the presence of oxidized iron (and manganese), no studies have yet directly quantified the amount of Fe^{3+} present around burrow structures and the role of benthic animals for iron and manganese respiration in sediments. Another intriguing question arises: is mineralization of refractory organic substrates with Mn^{4+} and Fe^{3+} as electron acceptors potentially faster than sulfate reduction as shown for aerobic respiration? Thus, Kristensen and Holmer[59] showed that the rate of mineralization with nitrate as electron acceptor is indistinguishable from the rate with sulfate reduction. These questions may be solved by mapping Mn^{4+} and Fe^{3+} distribution from vertical and radial burrow wall dissections combined with sediment incubations using a variety of aerobic and anaerobic techniques.

Bacterial populations. The microbial communities and associated diagenetic processes dominating in the oxic and oxidized zones around semipermanent burrows of infaunal species like *Nereis* spp. and *Arenicola marina* are usually considered identical to those in the equivalent zones at the sediment surface. However, the environmental conditions prevailing in burrows are basically different from those at the sediment surface. Burrows can be considered physically stable on a time-scale of days to weeks (lifetime of burrow structures) and chemically unstable on a scale of minutes (oxic–anoxic oscillations due to intermittent irrigation), whereas the sediment surface is physically unstable on a short-term scale (advective forces such as waves and currents) and chemically stable on a long-term scale (continuously oxic conditions in overlying water). Consequently, the specific environmental conditions may support the growth of different microbial communities in burrows and at the sediment surface.[69] Thus, despite an apparent similarity in the suite of microbial processes (oxic respiration, nitrification and denitrification) occurring in both environments, the volume specific activities may vary considerably.[70] This may be explained by different population sizes of the same microbial communities, or by the presence of specific microbial communities adapted to the physical and chemical conditions prevailing in the two environments. At present, there are no answers to these paradigms, but as studies have shown basic differences in the species composition of meiofaunal communities in the two environments,[71,72] a similar situation may occur for microorganisms as well. Recent advances in molecular biology have created a new array of methodologies for examining the population structure of microbial communities in natural environments.[73] Techniques such as gene probing and polymerase chain reaction (PCR) can provide a very specific and sensitive evaluation of similarities and differences in microbial communities. Microbiologists are now able to use small samples of microbial nucleic acids to identify unculturable bacteria, track genes, and evaluate genetic diversity in environmental samples. Although no studies have yet applied these techniques to burrow samples, they should, with adequate modifications, be reliable tools for describing variations of the microbial community structure in different sediment compartments.

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