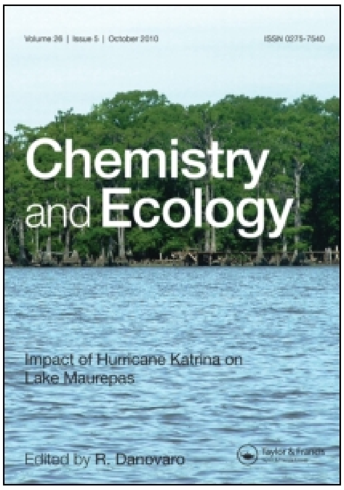

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IT'S A DIRTY JOB BUT SOMEONE HAS TO DO IT: THE ROLE OF MARINE BENTHIC MACROFAUNA IN ORGANIC MATTER TURNOVER AND NUTRIENT RECYCLING TO THE WATER COLUMN

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Benthic macrofaunal populations through their feeding, bioturbation, burrow construction and sediment irrigation activities have profound influences on organic matter inputs to marine sediments (biodeposition) and on the vertical distribution of deposited organic matter within the sediment. These effects in turn influence the rates and pathways of organic matter mineralisation, and element cycles. Similarly, bioturbation, burrow construction and burrow irrigation are major determinants of sediment-water column fluxes of oxygen and nutrients.

In this review, I discuss the influences of the different benthic macrofaunal feeding (functional) groups on mineralisation processes and sediment-water column fluxes of particulate and dissolved nutrients. How these effects influence diagenic processes, the balance between aerobic and anaerobic processes, and the redox status of the surficial sediments. Finally, I discuss some of the limitations of the predominantly laboratory techniques which have been used to study "macrofaunal effects" and how this hinders the inclusion of the effects in quantitative sediment biogeochemical models.

Keywords: Bioturbation; Nutrient recycling; Organic matter turnover; Diagenesis; Sediment-water column fluxes

1 INTRODUCTION

Primary production in shallow marine environments is generally considered to be nutrient (generally nitrogen) limited (Ryther and Dunstan, 1971; Eppley *et al.*, 1979; Smith, 1984) and is to a large extent dependent upon inorganic nutrients regenerated in the sediment compartment, so called benthic-pelagic coupling. Various studies have estimated that inorganic nitrogen regeneration in the sediment can provide between 20 and 100% of the annual nitrogen requirements for phytoplankton production in the water column in shallow coastal environments. For example, in Aarhus Bay, Denmark, release of nutrients from the sediments accounted for 29 and 16–19% respectively of the annual N and P demands for primary production in the water column, whereas terrestrial runoff and atmospheric inputs together accounted for only 16–21 and 4–9% of N and P requirements respectively (Jørgensen, 1996). Similarly, in a Danish Fjord, Kertinge Nor, which suffers from blooms of the green

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alga *Chaetomorpha linum*, annual P release from the sediments was 3.3 fold greater than total external (land and air) inputs and the net N release was equivalent to 40% of the external inputs (Riisgård *et al.*, 1996). Thus, particularly in well mixed coastal areas, rates of nutrient recycling in the sediments will influence rates of primary production in the overlying waters.

The benthic infauna through their feeding, bioturbation, burrow construction and burrow irrigation activities influence rates of organic matter inputs to the sediment, the vertical distribution of this organic matter, the rates and pathways of organic matter mineralisation within the sediment compartment and the fluxes of the regenerated dissolved nutrients back to the overlying water (Graf and Rosenberg, 1997; Kristensen, 1988; Aller, 1988; Hansen and Kristensen, 1998; Christensen *et al.*, 2000; Kristensen, 2000). The degree of these effects is in large part dependent upon the comportment of the individual species and in particular, their feeding mode. Therefore, the biomass, population density and community structure of the benthic fauna is a significant determinant of local nutrient recycling rates and hence influences primary production in the overlying water column, which in turn, ultimately represents the organic matter input to the sediment and the food source for the benthic community.

In this review, I discuss the mechanisms by which the faunal community influences organic matter inputs to the sediment, turnover of this material in the sediment and the composition and rates of efflux of the regenerated nutrients back to the water column.

2 INFLUENCE OF THE MACROFAUNA ON ORGANIC MATTER MINERALISATION

As indicated in the introduction, the feeding mode of the individual species to a large extent determines their comportment and consequently their influence on biogeochemical process. Therefore, initially the different feeding groups are considered separately. However, it should be noted that these feeding modes are somewhat arbitrary and not mutually exclusive, and many organisms are able to rapidly alternate between feeding modes. For example, *Polydora* sp. form small projecting tubes at the sediment surface through which protrude fine tentacles which trap particles from the water column (suspension-feeding) or scour the sediment selectively picking-up organic particles (surface deposit-feeding) (Hylleberg and Henriksen, 1980). Similarly *Corophium volutator* may simultaneously surface deposit and suspension feed (Gerbol and Hughs, 1994), whilst, other species may switch between feeding modes dependent upon relative food availability. For example, when phytoplankton concentrations in the water column are high ($1\text{–}3\ \mu\text{g chl a l}^{-1}$) the deposit-feeding *Nereis diversicolor* spins a mucus net at the head of its burrow and initiates cycles of suspension-feeding by pumping water through the net, which is periodically ingested and replaced (Vedel *et al.*, 1994) and in spionid polchaetes the switch between surface deposit and suspension-feeding modes is dependent upon current speeds (Taghon, 1992).

2.1 Surface and Sub-surface Deposit Feeders

Surface and sub-surface deposit feeders influence organic matter mineralisation and nutrient regeneration rates mainly through the mechanical breakdown of particulate matter, which increases the total surface area available for bacterial colonisation, and through the mixing of freshly deposited particulate organic matter into the deeper sediment strata (Yingst and Rhoads, 1980; Aller, 1994; Sandnes *et al.*, 2000). Typical sub-surface "conveyor belt" feeders are intense bioturbators and can cause deep irrigation by injecting water into the feeding pocket, which then percolates back to the sediment surface (Rijken, 1979; Hüttel, 1990; Rasmussen *et al.*, 1998). These organisms inhabit more or less permanent, vertical burrows feeding upon the anoxic sub-surface sediments which are transported to and deposited at the sediment surface as faecal castings. Thus, porewater nutrients and accumulated reduced compounds are transported to the surface where they can be released or re-oxidised, whilst particulate organic matter, oxygen and other electron acceptors are pumped into the deeper anoxic sediment strata (Rijken, 1979; Aller, 1994; Hüttel, 1990; Rasmussen *et al.*, 1998; Banta *et al.*, 1999). Consequently, these bioturbated sediments do not exhibit a classical unidirectional redox succession with increasing depth, but a continually shifting mosaic of aerobic, suboxic and anaerobic micro-zones (Fenchel, 1996; Kristensen, 2000; Kristensen and Holmer, 2001; see also Fig. 1).

In contrast surface deposit feeders, feed on organic detritus deposited on the sediment surface and benthic microalgae (when present), and this material is transferred into the deeper sediment layers. Surface deposit-feeding polychaetes and crustaceans commonly inhabit more or less "U" shaped burrows, whilst bivalves are permanently buried with their siphons extended to the sediment surface (Rhoads, 1974; Kristensen, 1988). The burrows are intermittently irrigated with oxygenated water pumped from the water column in order to support the inhabitants respiratory needs. Unlike sub-surface deposit feeders, sediment reworking is not directly associated with feeding in surface deposit feeders, but with the construction, maintenance and extension of their burrow structures.

In addition the burrow structures formed by infaunal surface and sub-surface deposit feeders also exert a major influence on the exchange of substrates and nutrients between the sediment and the water column. Burrow structures significantly increase the total sediment surface area available for diffusive exchanges, with increases for natural estuarine populations estimated at between 150–500% (Hylleberg and Henriksen, 1980; Kristensen, 1984; Forster and Graf, 1992; Davey, 1994; Fenchel, 1996), *i.e.* below each m^2 of sediment, there are between 1.5 and $5\,m^2$ of burrow surfaces. The irrigation of these burrows by the animals to support their respiratory oxygen demands, flushes accumulated nutrients to the water column, replenishes pools of water column derived substrates and maintains

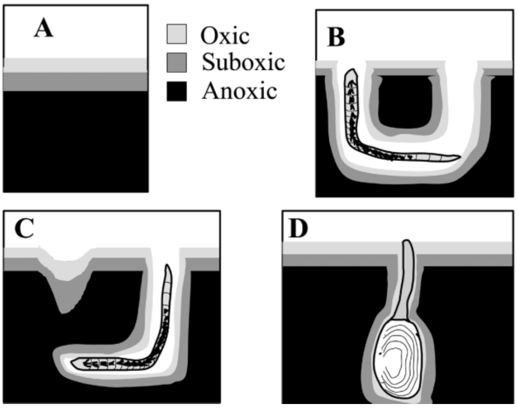

FIGURE 1 Idealised distributions of sediment redox zones in an uncolonised sediment (A) where respiration processes are diffusion controlled, and around the burrows of a surface deposit-feeding polychaete (B), a sub-surface feeding polychaete, feeding draws oxidised sediment down through the feeding pit (C) and an infaunal filter-feeding bivalve (D). The oxic zone is the sediment zone where oxygen is present, in the suboxic sediment, oxygen is not present, but the sediment is not reduced and bacterial respiration is supported by nitrate and oxidised metals (iron and manganese). Whereas, the anoxic sediment is oxygen-free and reduced as bacterial respiration is dominated by sulfate reduction.

concentration gradients between the sediment porewater and the burrow water favouring further diffusive exchanges (Aller, 1988; Kristensen, 1988; Forster and Graf, 1995; Aller and Aller, 1998).

However, whilst the feeding, sediment reworking and burrow irrigation activities of deposit feeders will influence organic matter turnover, nutrient regeneration rates and sediment-water column fluxes of dissolved materials, they have little effect on overall organic matter inputs to the sediment and are primarily dependent on the natural sedimentation of organic matter from the water column (Christensen *et al.*, 2000). Although the effects of structures such as feeding pits or towers extending above the sediment surface may have some influence on water movement and hence sedimentation rates (Rhoads *et al.*, 1978; Yager *et al.*, 1993; Graf and Rosenberg, 1997).

2.2 Suspension Feeders

In common with surface and sub-surface deposit feeders, suspension feeders stimulate rates of organic matter turnover and nutrient regeneration in the sediment, and enhance sediment-water column fluxes of nutrients through direct excretion of nutrients, and the formation and irrigation of burrows in species which construct such structures. However, the degree of these effects differ greatly, as unlike deposit feeders which intermittently ventilate their burrows, suspension feeders ventilate their burrows almost continuously in order to feed and thus have a more profound effect on nutrient and substrate exchanges (Kristensen, 1989; Riisgård, 1991; Christensen *et al.*, 2000; Kristensen, 2000). Moreover, suspension feeders not only stimulate rates of organic matter mineralisation and sediment-water column fluxes of dissolved materials through their bioturbation and ventilation activities, but can also significantly increase overall organic matter inputs to the sediment, as particulate matter is actively concentrated from the water column and deposited in the sediment as faeces and pseudofaeces (Yamamuro and Koike, 1993; Vedel *et al.*, 1994; Graf and Rosenberg, 1997). For example, in comparative laboratory experiments the facultative suspension feeder *Neries diversicolor* (Polychaeta) increased phytoplankton deposition rates 30-fold compared to the closely related surface deposit-feeding species, *Neries virens* or defaunated controls (Christensen *et al.*, 2000) and *in situ* rates of organic carbon and nitrogen inputs to sediments near to (0–10 cm) individuals of the large suspension-feeding bivalve *Atrina zelandica* were higher than in more distant (>30 cm) sediments, and the sediments close to the bivalves were enriched in carbon and nitrogen compared to more distant sediment zones (Norkko *et al.*, 2001).

In shallow water environments, the high filtration capacities of the macrofauna populations are such that the entire water column can potentially be filtered in periods of one to a few days. It has been proposed that such high filtration capacities are sufficient to regulate phytoplankton growth in the water column (Officer *et al.*, 1982; Cohen *et al.*, 1984; Hily, 1991; Riisgård *et al.*, 1996) and may represent a natural eutrophication control system (Officier *et al.*, 1982; Cloern, 1982; Cohen *et al.*, 1984; Nakamura and Kerciku, 2000; Cloern, 2001). Although, this hypothesis does not take into account the rapid nutrient cycling associated with dense populations of suspension feeders, which would tend to favour further primary production in the water column (Dame *et al.*, 1984; Boucher and Boucher-Rodoni, 1988; Dame and Dankers, 1988; Asmus and Asmus, 1991; Magni *et al.*, 2000). Indeed, dense beds of suspension feeders may cause localised eutrophication by concentrating the deposition of particulate materials produced in adjacent marine areas or transported by terrestrial runoff within confined areas, creating "hot spots" of nutrient loading and recycling. However, although benthic suspension feeder communities have long been known to have a highly significant effect on phytoplankton and suspended particle fluxes, few reliable direct measurements of biodeposition rates exist, due to the difficulties in distinguishing the contributions of direct biodeposition, indirect biodeposition resulting from the effects of macrofaunal structures and epibenthic organisms on water movement, and natural sedimentation rates, to overall deposition rates in natural environments (see Graf and Rosenberg, 1997, for review). Measured rates of biodeposition vary markedly, depending upon the density and composition of the animal communities, and the availability and quality of seston in the overlying water, but fall within the range of 1–70 g carbon $m^{-2}\,d^{-1}$ (Graf and Rosenberg, 1997), with the higher values generally associated with dense banks of filter-feeding bivalves such as oysters and mussels. Thus, suspension feeders in addition to stimulating rates of nutrient regeneration by enhancing rates of organic matter turnover, also stimulate rates by increasing the overall input of organic matter and hence nutrient loads to the sediments.

2.3 Role of the Macrofauna in Organic Matter Turnover and Nutrient Recycling

As discussed in the preceding sections benthic macrofauna have a profound influence upon the inputs of organic matter to the sediment and through bioturbation, its depth distribution within the sediment. Modelling exercises and microcosm studies on the effects of organic matter loads and distributions in defaunated, sieved sediments indicate that both these influences are important determinants not only of overall organic matter mineralisation rates, but also of the pathways by which the organic matter is mineralised (Blackburn and Blackburn, 1993a,b,c; Caffrey *et al.*, 1993; Sloth *et al.*, 1995; Blackburn, 1996). The mixing of "fresh" organic matter into the sediment by bioturbation is proposed to enhance overall carbon mineralisation rates mainly through stimulation of the mineralisation of the "older" more recalcitrant organic matter already present in the sediment (Andersen and Kristensen 1988; Kristensen *et al.*, 1992).

This effect was clearly apparent in microcosm studies of the degradation of ^{14}C labelled microalgae in cores containing macrofauna and defaunated controls (Andersen and Kristensen, 1992). Whilst, in these experiments, there was a pulse release of ^{14}C labelled CO_2 and dissolved organic carbon (DOC) in cores containing macrofauna, compared to controls over the first 4 days of incubation, over the entire 21 day incubation period, the total release of ^{14}C-labelled mineralisation products was similar for both treatments and controls. However, overall organic matter mineralisation rates, measured as total CO_2 production in the microcosms, were 70% higher in cores containing macrofauna compared to defaunated controls (Andersen and Kristensen, 1992). Similar results were also obtained in equivalent microcosm incubations with and without the surface deposit-feeding polychaete *Nereis diversicolor*, to which ^{14}C-labelled macroalgal detritus (*Chondrus crispus*) was added (Kristensen *et al.*, 1992). Again, there was little difference between $^{14}C\text{-}CO_2$ production rates over the 20 day incubation period in microcosms with and without *N. diversicolor* at 3 different temperatures, but the presence of *N. diversicolor* stimulated total CO_2 production by 30–40%. The discrepancies between the macrofaunal effects on fluxes of labelled and unlabelled products in these experiments indicates that the surface deposit feeders studied, preferentially stimulated the mineralisation of "older" refractory organic substrates already present in the sediment, rather than that of the freshly deposited microalgal or macroalgal biomasses.

The enhancement of turnover rates of refractory organic substrates may be related to two principal factors. Firstly, the introduction via bioturbation of labile organic substrates into the deeper sediment strata may allow bacteria to co-metabolise more recalcitrant substrates already present in these strata (Schink, 1988; Graf, 1992). Secondly, as well as increasing transport rates of organic matter to the deeper sediments, the macrofauna also enhance the transport of more powerful oxidants such as oxygen and nitrate to the same normally anoxic sediment strata (see Sec. 3), stimulating overall aerobic respiration rates and potentially the relative contribution of aerobic respiration to total respiration, as oxygen fluxes may be stimulated to a greater extent than carbon oxidation rates (Andersen and Kristensen, 1988; Aller, 1988; Banta *et al.*, 1999).

There has been some controversy concerning the relative efficiencies of aerobic and anaerobic metabolisms (see Kristensen, 2000, for a recent review), as several studies have found little difference in the mineralisation rates of fresh organic material under aerobic and anaerobic conditions (*e.g.* Hansen and Blackburn, 1991; Andersen, 1996). However, degradation rates of certain substrates such photosynthetic pigments (Sun *et al.*, 1993), lipids (Harvey *et al.*, 1995), fatty acids (Sun *et al.*, 1997) and complex polymers such as lignin (Benner *et al.*, 1984) are significantly faster under aerobic compared to anaerobic conditions. Similarly, recent studies of the degradation of "aged" diatom biomasses under aerobic and anaerobic conditions have demonstrated that degradation rates are between 5 and 10 fold higher during aerobic compared to anaerobic mineralisation (Kristensen *et al.*, 1995; Andersen *et al.*, 1996; Kristensen and Holmer, 2001). Additionally, Aller (1994) has proposed that the cyclic oscillations between aerobic and anaerobic micro-zones caused by the particle reworking activity of bioturbating fauna results in both more complete and sometimes faster mineralisation rates than is possible under constant conditions.

Thus, the activities of the benthic macrofaunal community are not only important in regulating overall rates of benthic metabolism. But as a consequence of their preferential stimulation of the mineralisation rates of the more refractory components of the sediment organic matter pool, their activities may also influence overall carbon burial rates in marine sediments.

A similar macrofaunal enhancement of nitrogen regeneration rates by surface deposit-feeders has also been observed in meso- and microcosm experiments, with gross rates of N-mineralisation in the sediment and the efflux of mineralisation products to the water column being stimulated up to 4-fold in the presence of animals (Kristensen and Blackburn, 1987; Hansen and Blackburn, 1992; Hansen and Kristensen, 1997; Hansen and Kristensen, 1998; Christensen *et al.*, 2000). For example nitrogen mineralisation rates were stimulated 1.6-fold in microcosms containing *Neries virens*, with mineralisation rates over the 94 day incubation averaging 76 and 47 $\mathrm{nmol\,N\,cm^{-3}}$ sediment $\mathrm{d^{-1}}$ respectively, in the presence and absence of *N. virens* (Kristensen and Blackburn, 1987).

The presence of suspension feeders would further enhance rates of overall sediment metabolism and inorganic nitrogen regeneration, as a result of the increased inputs (biodeposition) of organic matter to the sediments as faeces and pseudofaeces. The influence of suspension feeders on nitrogen cycling has been particularly intensively studied for suspension-feeding bivalves and especially for dense commercially exploited mussel beds and oyster banks (*e.g.* Dame *et al.*, 1984; Dame and Dankers, 1988; Boucher and Boucher-Rodoni, 1988; Asmus and Asmus, 1991). In these systems net ammonium fluxes ranged from 0.1 to 0.5 (Dame *et al.*, 1984), 2.9–7.9 (Dame and Dankers, 1988), 0.1 to 0.4 (Boucher and Boucher-Rodoni, 1988) and -5 to 20 $\mathrm{mmol\,m^{-2}\,h^{-1}}$ (Asmus and Asmus, 1991) dependent upon seasonal changes in temperature, seasonal and tidal variability in seston availability, and at least in the case of the study of Asmus and Asmus (1991), by diurnal changes in ammonium assimilation rates by epiphytic brown algae growing on the mussel beds. Similarly, high nitrogen fluxes have also been reported for natural dense populations of suspension-feeding infaunal bivalves, such as *Cardium edule* and *Mya arenaria* (Loo and Rosenberg, 1989), and *Corbicula japonica* (Yamamuro and Koike, 1994; Nakamura and Kerciku, 2000). However, even at low densities the effects of suspension-feeding bivalves can be significant, for example in long term mesocosm experiments, the presence of the hard clam *Mercenaria mercenaria* at a density of only 16 ind. $\mathrm{m^{-2}}$ stimulated dissolved inorganic nitrogen fluxes to the water column by on average 57% (Doering *et al.*, 1987). Thus, especially in shallow water ecosystems, the benthic macrofauna and particularly suspension feeders significantly stimulate rates of nitrogen recycling and the return of inorganic nitrogen species to the water column, potentially enhancing primary production processes, which in turn would increase seston availability for suspension feeders and consequently organic matter inputs to the sediment system.

As well as augmenting overall rates of nitrogen regeneration, the benthic macrofauna also influence the relative balance between the nitrogen species, dissolved organic nitrogen (DON), ammonium, nitrate, nitrite and molecular dinitrogen which are returned to the water column. Modelling exercises and microcosm simulations have shown that the magnitude of organic matter inputs and the depth distribution of the organic matter within the sediment are important determinants of both the quantity and the chemical composition of the nitrogen returned to the water column (Blackburn and Blackburn, 1993a,b,c; Caffrey *et al.*, 1993; Sloth *et al.*, 1995; Blackburn, 1996).

In the absence of bioturbation, deposited organic matter would be mineralised at or near to the sediment surface and much of the initial breakdown products, DON and ammonium would escape to the water column before being further oxidised (Sloth *et al.*, 1995; Blackburn *et al.*, 1996). Increasing organic matter inputs to the sediment surface, increase overall dissolved nitrogen effluxes from the sediment and the relative contribution of DON and ammonium to the overall N-efflux (Blackburn and Blackburn, 1993a; Sloth *et al.*, 1995). Under these conditions nitrification (ammonium oxidation to nitrate) rates are initially stimulated by increased organic matter inputs due to increased ammonium availability, but at high organic matter inputs nitrification is inhibited, due to reduced oxygen penetration into the sediment and increased competition with heterotrophs for the available oxygen. Consequently, most of the regenerated ammonium escapes to the water column without being oxidised (Blackburn and Blackburn, 1993a; Sloth *et al.*, 1995; Blackburn, 1996). Denitrification rates coupled to nitrification closely follow nitrification rates (Blackburn, 1996), whereas denitrification of nitrate diffusing from the water column is stimulated at higher organic matter inputs, due to the lower oxygen penetration into the sediment and consequently shorter diffusional path-length for nitrate from the water column to the denitrification zone. Therefore, the net effect of high organic matter inputs to the sediment surface on overall denitrification rates is highly dependent upon the water column nitrate concentration *i.e.* whether the inhibition of coupled nitrification-denitrification is greater or less than the stimulation of denitrification of nitrate from the water column, which in turn is a function of nitrate availability in the water column. Additionally, at very high organic matter loads, especially if nitrate availability is low, the high ratio of electron donors to electron acceptors may favour dissimilatory nitrate reduction to ammonium (DNRA) over denitrification as a sink for nitrate (Tiedje, 1987). DNRA represents an internal shunt in the nitrogen cycle favouring nitrogen retention within the system by recycling nitrate that might otherwise be denitrified.

In contrast during model and microcosm simulations under mixed (bioturbated) conditions, most organic matter degradation takes place at depth in the sediment and the mineralisation products diffuse towards the sediment surface. During this slow diffusion process most DON is ammonified and little or no DON effluxes from the sediment (Blackburn, 1996). Before exiting the sediment the generated ammonium must cross the surficial aerobic sediment layer, where it is in part nitrified to nitrite and nitrate, which can efflux from the sediment or diffuse back to anaerobic zones and be eliminated as gaseous N_2 by denitrifying bacteria. Thus, under mixed conditions a greater proportion of the mineralised particulate organic nitrogen would be returned to the water column as inorganic compounds (ammonium, nitrite and nitrate) or be eliminated from the system as gaseous products (NO, N_2O

and N_2) via nitrification and denitrification (Blackburn and Blackburn, 1993a,b,c; Caffrey *et al.*, 1993; Sloth *et al.*, 1995; Blackburn, 1996). As in the case of surface deposited organic matter, nitrification rates and hence rates of coupled nitrification–denitrification are favoured by moderate inputs of organic matter due to increased ammonium availability, whereas at high organic matter inputs nitrification is limited by oxygen availability and at low inputs by ammonium limitation (Blackburn and Blackburn, 1993; Caffrey *et al.*, 1993; Sloth *et al.*, 1995; Blackburn, 1996). However, for any given organic matter input rate, a greater proportion of the mineralised nitrogen is nitrified and subsequently denitrified under mixed conditions compared to when organic matter mineralisation takes place only at the sediment surface (Blackburn and Blackburn, 1993a,b,c; Caffrey *et al.*, 1993; Sloth *et al.*, 1995; Blackburn, 1996).

In addition to influencing nitrification and denitrification rates through the mixing of organic matter into the sediments during bioturbation, the construction of burrows and the irrigation of these with oxygenated water also significantly stimulates nitrification rates. As discussed previously, below each m^2 of sediment, there may be between 1.5 and 5 m^2 of burrow surfaces (Hylleberg and Henriksen, 1980; Kristensen, 1984; Forster and Graf, 1992; Davey, 1994; Fenchel, 1996). The presence of these burrow surfaces greatly increases the total volume of oxic sediment in which nitrification can occur and the area of oxic/anoxic interfaces over which nitrate diffusing from the burrow water or generated via nitrification can reach the anoxic denitrification zones. Moreover, the wall sediments of infaunal burrows have been proposed to be a privileged site for nitrifying bacteria due to the high availability of ammonium diffusing from the adjacent anoxic sediments and oxygen from the burrow water. Several authors have reported that the potential nitrification rates of burrow wall sediments are up to 1–2 orders of magnitude higher than those of the oxic surface sediments at the same site (Henriksen *et al.*, 1983; Kristensen *et al.*, 1985; Mayer *et al.*, 1995; Kristensen, 2000) and a recent study has also demonstrated high rates of potential nitrification associated directly with the surfaces of the animals themselves (Welsh *et al.*, submitted; Fig. 2).

Numerous investigations have also demonstrated that the presence of burrow forming macrofauna stimulates rates of nitrification, coupled nitrification–denitrification and denitrification of water column nitrate (*e.g.* Henriksen *et al.*, 1980; Sayama and Kurihara, 1983;

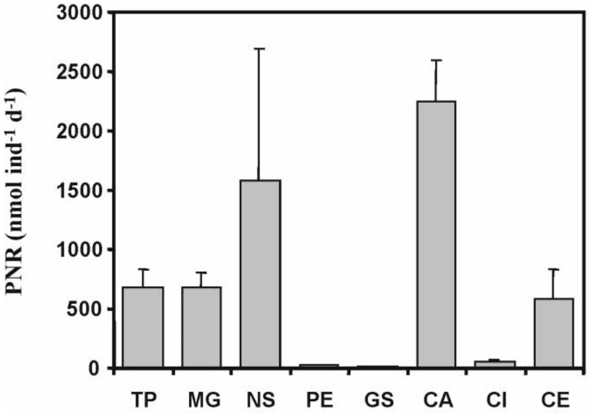

FIGURE 2 Potential nitrification rates (PNR) associated with the isolated marine benthic organisms *Tapes philippinarum* (TP), *Mytilus galloprovincialis* (GP), *Neanthes succinea* (NP), *Palaemon elegans* (PE), *Gammerus* spp. (GS), *Carcinus aestuari* (CE), *Corophium insidiosum* (CI) and *Cyclope neritea* (CN). Data from Welsh *et al.* submitted.

Kristensen *et al.*, 1991; Henriksen *et al.*, 1993; Pelegrí *et al.*, 1994; Pelegrí and Blackburn, 1995; Rysgaard *et al.*, 1995; Nizzoli *et al.*, 2002). Thus, the presence of burrowing macrofauna will result in a further shift in the speciation of the products of organic-N mineralisation towards nitrate and N_2, compared to that predicted from model and microcosm simulations where only the bioturbation (mixing) effect of the macrofauna is included, but not the effects of burrow wall surfaces and burrow irrigation.

3 INFLUENCE OF THE MACROFAUNA ON SEDIMENT-WATER COLUMN NUTRIENT AND OXYGEN FLUXES

The biomass, density and species (functional group) composition of the macrofaunal community can influence fluxes of dissolved organic and inorganic species between the sediment and water column via three principal mechanisms. Firstly, as discussed in the previous sections the macrofauna influence organic and inorganic nutrient fluxes to the water column through their effects on organic matter deposition rates and the depth distribution of this organic matter in the sediment. The combination of these effects controls nutrient regeneration rates and thereby the size of the porewater dissolved nutrient pools which can potentially flux to the water column, and the concentration gradient of the dissolved species between the porewater and water column, which is one of the most important determinants of diffusive flux rates (Berg, 1983; Cussler, 1989; Blackburn and Blackburn, 1993).

Secondly, the macrofauna directly influence benthic fluxes of oxygen and dissolved nutrients through their metabolism. Oxygen is actively taken up to support the animals respiration and metabolic end-products, such as ammonium, urea and phosphate are excreted directly to the water column or into the burrow water, and later flushed to the water column during burrow irrigation. The contribution of the direct excretion of ammonium to overall sediment-water column fluxes has been estimated by incubating individual animals and extrapolating the ammonium excretion data to field densities or animal densities in mesocosms. These data indicate that this contribution can be highly significant, with animal ammonium excretion rates potentially accounting for between 10 and 70% of the total ammonium or dissolved inorganic nitrogen efflux to the water column (Blackburn and Henriksen, 1983; Kristensen, 1988; Loo and Rosenberg, 1989; Gardener *et al.*, 1993). Similarly, macrofaunal specific phosphate excretion rates can also be high (Tab. I) and potentially could be a major

TABLE I Specific Ammonium and Phosphate Excretion Rates of Some Infaunal and Epifaunal Benthic Marine Invertebrates.

Family/species	*Temp (°C)*	*Ammonium (μmol g DW^{-1} h^{-1})*	*Phosphate (μmol g DW^{-1} h^{-1})*	*References*
Ruditapes philippinarum	20–22	3.8–10.6	0.7–3.9	Magni *et al.*, 2000
Musculista senhousia	20–22	9.3–16.9	1.3–5.5	Magni *et al.*, 2000
Echinodea	5–10	1.2	0.2	Blackburn and Henriksen, 1993
Ophiuroidea	5–10	3.7	0.5	Blackburn and Henriksen, 1993
Polycheata	5–10	5.0	1.6	Blackburn and Henriksen, 1993
Lamellibranchia	5–10	2.1	0.8	Blackburn and Henriksen, 1993
Magelona sp.	20–23	27.0–53.1	ND	Gardener *et al.*, 1993
Paraprionaspio pinnata	20–23	5.9–12.6	ND	Gardener *et al.*, 1993
Capitellidae sp.	20–23	0.7	ND	Gardener *et al.*, 1993
Nereis sp.	20–23	2.3	ND	Gardener *et al.*, 1993
Ampelisca abdita	20–23	5.4	ND	Gardener *et al.*, 1993
Ampelisca vadorum	20–23	3.2	ND	Gardener *et al.*, 1993

determinant of sediment-water column phosphate fluxes. However, sediment phosphate release/retention dynamics are highly dependent upon sediment redox status, as oxidised metal complexes, such as iron and manganese oxyhydroxides are able to chemically bind inorganic phosphate, which may subsequently be released to the porewater if the metal is reduced (Sundby *et al.*, 1992; Jensen *et al.*, 1995; Slomp *et al.*, 1996; Föllimi, 1996). Due to these redox sensitive retention/release dynamics it is difficult to correlate macrofaunal phosphate excretion rates directly with sediment-water column phosphate fluxes (Blackburn and Henriksen, 1983), as relationships are obscured by redox shifts in the sediment, which induce a net release or retention of phosphate in the metal bound pools. Macrofaunal respiration can also be a major determinant of overall benthic oxygen demand. For example, in mesocosm experiments simulating sediment recolonisation by nereid worms, the animal's respiratory oxygen consumption was estimated to account for between 20 and 40% of total sediment oxygen demand, and 30–50% of the increase in oxygen uptake induced by the worm additions (Hansen and Kristensen, 1997; Nizzoli and Welsh, 1999; see also Fig. 3).

Thirdly, the benthic macrofauna also stimulate sediment-water column fluxes of dissolved species through bioturbation and the construction of burrow structures. Bioturbation physically mixes the sediment and porewater causing vertical transport of dissolved solutes at rates very much greater than could be achieved by diffusion alone (Powilliet *et al.*, 1994; Berg *et al.*, 2001). Whereas, the construction of burrows stimulates exchanges between the sediment and water column by increasing the total sediment surface area in contact with the water column and therefore available for diffusive exchanges by up to 500% (Hylleberg and Henriksen, 1980; Kristensen, 1984; Forster and Graf, 1992, Davey, 1994; Fenchel, 1996).

The degree of stimulation of diffusive exchanges as well as been dependent upon the increased surface area offered by the burrow walls, is also regulated by the concentration gradients of individual solutes between the porewater of the burrow wall sediments and the water within the burrows (Berg, 1983; Cussler, 1989), and the diffusive properties of the burrow walls themselves (Aller, 1983). In general, macrofaunal burrows have some form of lining and the form of this lining will influence diffusive exchanges. Burrow linings range from the simple mucus secretions of some nereid worms to the resistant, parchment-like linings

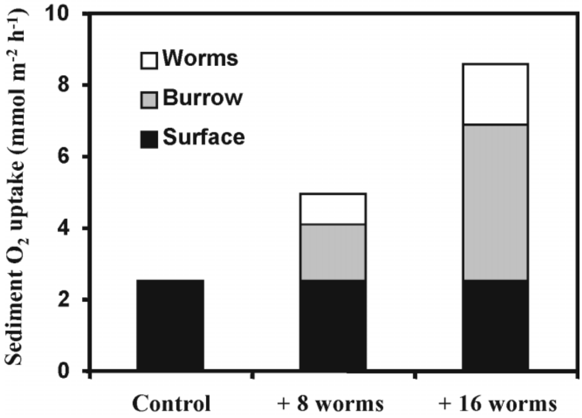

FIGURE 3 Contribution of worm respiration, burrow wall sediments and surficial surface sediments to total benthic oxygen uptake in sediment cores supplemented with 0, 8 and 16 individuals of the surface deposit-feeding polychaete *N. succinea*. Worm additions were equivalent to 1600 and 3200 ind m^{-2}. For details of the incubations and calculations see Nizzoli and Welsh, 1999.

produced by some polycheates (Defretin, 1971; Kristensen, 1988; Kristensen *et al.*, 1991). Similarly, the burrows of bivalves are also normally lined with mucus and in this case, the animals siphons, when extended within the burrows also represent an additional and selective barrier to diffusion (Pelegrí and Blackburn, 1995). In a study of the properties of the burrow linings of eight marine infaunal species, Aller (1983) found that the diffusive permeability of the burrow wall linings ranged between 10 and 40% of that in free solution and would have a large influence of diffusive fluxes.

Concentration gradients between the porewater and burrow water, which are the driving force for diffusive exchanges are dependent upon the dynamic equilibrium between the production, consumption and loss processes for the specific solute in the sediment, which regulate porewater solute concentrations, and the concentration of the solute in the burrow water. Solute concentrations in the burrow water in turn are dependent on their concentrations in the overlying (input) water, the residence time of the water within the burrow and the depletion or accumulation dynamics of the specific solute in the burrow due to diffusive exchange with the sediment, and rates of consumption or excretion of the solute by the resident animal.

Burrow irrigation by infaunal animals is an intermittent process with phases of active irrigation alternating with rest periods over more or less rhythmical cycles (Kristensen, 1989; Riisgård, 1991; Winsor *et al.*, 1990; Forster and Graf, 1995; Christensen *et al.*, 2000). The relative lengths of the irrigation and rest periods, and the intensity of active irrigation is highly variable with species, but suspension feeders which are dependent upon the ventilated water for both their oxygen and food requirements tend to irrigate more intensely and for a greater proportion of time than deposit feeders which rely on the irrigation water only for their respiratory oxygen demands (Jørgensen, 1975). For example, in the closely related polychaete species, *Neries virens* and *N. diversicolor*, the surface deposit-feeding *N. virens* irrigates its burrow for periods of 5–8 minutes separated by resting phases of approximately 30 minutes (Kristensen, 1989), whereas, when suspension-feeding *N. diversicolor* irrigates its burrow semi-continuously with only short pauses of a few minutes (Riisgård, 1991). Not only does *N. diversicolor* irrigate its burrow more continuously than *N. virens*, but irrigation rates for similar sized individuals of *N. diversicolor* are approximately 4-fold higher than those for *N. virens* (Christensen *et al.*, 2000). Consequently, in mesocosm experiments in which $\sim$400 mg fresh weight individuals of *N. diversicolor* or *N. virens* were added to a density of $600\,\mathrm{ind\,m^{-2}}$, total sediment irrigation rates were estimated to be 2700 ± 185 and $179 \pm 8\,\mathrm{l\,m^{-2}\,d^{-1}}$ respectively, for the suspension-feeding *N. diversicolor* and surface deposit-feeding *N. virens* populations (Christensen *et al.*, 2000).

Such large differences in the intensity and rhythms of burrow irrigation have significant implications for diffusive fluxes between the sediment porewater and the burrow water, and therefore for overall sediment-water column solute fluxes. Intense burrow irrigation results in a rapid turnover (short residence time) for the burrow water and will favour diffusive exchanges, by maintaining high solute concentration gradients across the burrow walls. In contrast, in weakly irrigated burrows, water residence time will be longer, solutes diffusing from the sediment or excreted by the animals will accumulate in the burrow water and the concentration of solutes in the burrow water which are consumed by the animal or burrow wall sediments will decline. Therefore, solute concentrations in the burrow water and porewater will tend towards equilibrium and net solute fluxes will decline as the concentration gradient of the solute between burrow and porewater declines. Due to these depletion and accumulation processes for solutes, there may also be significant spatial variation of solute fluxes along the length of the burrow especially at low irrigation rates. Since, during passage through the burrow, the solute composition of the burrow water will tend towards that of the porewater, reducing the gradients for further diffusive exchanges in the terminal parts of the burrow system. Similarly, since burrow irrigation is an intermittent process, there will also be temporal changes in fluxes across the burrow walls as the chemical composition of the burrow water changes with time. During pauses in burrow irrigation, flux rates would tend to decline as solute concentrations in the porewater and burrow water equilibrate, inhibiting further net diffusive exchanges, and resulting in an accumulation in the porewater of solutes such as ammonium and CO_2, which are generated from organic matter mineralisation in the sediment[1]. When burrow irrigation recommences there will be an initial pulse of solute fluxes as large concentration gradients are re-established between the porewater and the "fresh" burrow water, and solutes accumulated in the porewater during the pause will be flushed from the porewater. Thereafter, as the irrigation period proceeds, flux rates would progressively decline as the porewater pools are depleted and a new steady state is established between solute production rates and loss processes.

Such spatial and temporal differences in fluxes across the burrow walls, would be even greater in animals such as decapods, which form complex subterranean galleries rather than the simple U-shaped burrows formed by polychaete worms. These burrows may penetrate up to 1 m into the sediment and are composed of numerous interconnected inlets, turning chambers, vertical shafts and several tiers of lateral burrows, many of which are dead ends (Witbaard and Duineveld, 1989; Forster and Graf, 1995; Nickell and Atkinson, 1995). Compared to simple burrows, these structures have large volumes compared to the size of their inhabitants and water residence times can be extremely long and are variable between different parts of the burrow system. For example, the deposit-feeding thalassinidian shrimp *Callianassa subterranea* creates complex burrows with a mean total length of ~300 cm and a mean volume of ~150 ml (Forster and Graf, 1995). During respiratory irrigation, the shrimp ceases processing sediment in the lower parts of the burrow, positions itself below one of the burrow inlets and creates a "breathing current" by beating its pleopods. These irrigation events occur at roughly 40 minute intervals and last on average 2.5 minutes, in which time 4.5 ml (equivalent to 3% of the burrow volume) of water is pumped into the burrow. Individuals also repeatedly utilise a single burrow inlet for respiratory irrigation over periods of days and flow at one inlet has little effect on intersecting portions of the burrow (Forster and Graf, 1995). Thus, the water in much of the burrow system may remain unchanged for long periods of time, completely inhibiting fluxes as solute concentrations equilibrate across the burrow walls.

In addition to the quantitative effects on sediment-water column fluxes discussed above, animal burrows also qualitatively influence fluxes due to changes in source-sink relationships induced by the colonisation of the burrow walls by specific bacterial groups, such as nitrifying and denitrifying bacteria (see Sec. 2.3). However, as for overall diffusive exchanges, these qualitative changes in flux composition will also exhibit temporal variations dependent upon the irrigation cycles of the burrow inhabitant, due to changes in the bacterial activities. Since, as discussed in the preceding paragraphs, the availability of bacterial substrates such as oxygen, nitrate and ammonium in the burrow and porewaters will vary over irrigation cycles.

4 INFLUENCE OF THE MACROFAUNA ON SEDIMENT REDOX STATUS

Potentially, the activities of the benthic macrofauna could influence sediment redox status in both directions. Increased organic matter inputs to the sediment via direct and indirect biodeposition and enhanced rates of organic matter turnover through the transport of organic

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[1] Assuming organic matter mineralisation rates remain constant, production rates of solutes generated during this mineralisation are also unaltered, but diffusive losses of solute to the burrow water have declined, resulting in a net accumulation of the solutes in the sediment porewater.

matter into the deeper sediment strata, stimulate overall benthic metabolism and could favour anaerobic metabolisms which cause decreased redox status, if their reduced end products accumulate. Whereas, bioturbation, the increased surface area offered by burrow surfaces and burrow irrigation enhance oxygen transfer to the sediment and may promote aerobic over anaerobic respiration, and stimulate the re-oxidation of reduced compounds in the sediment, improving overall redox status. Consequently, the net effect of the macrofauna will be determined by the balance between these two conflicting influences *i.e.* the relative stimulation of total respiration compared to aerobic respiration, which as for many other macrofaunal effects, will be largely determined by the organisms functional group.

Whilst, numerous studies have quantified the influence of the macrofauna on sediment water column oxygen and nitrogen fluxes, with the exception of studies focussing on denitrification processes, very few have directly addressed macrofaunal effects on anaerobic metabolism and sediment redox conditions. In an early study, Aller and Yingst (1978) reported elevated rates of sulfate reduction in the burrow walls of the polycheate *Amphirite ornate* and hypothesised that increases in benthic metabolism associated with burrowing infauna would result principally from the stimulation of sulfate reduction. Similarly, Hines and Jones (1985) reported higher sulfate reduction rates in bioturbated compared to non-bioturbated sediments in Great Bay, New Hampshire, which they attributed to the continual mixing of fresh reactive organic matter into the sediment by the macrofauna. In contrast, during microcosm experiments in which the sub-surface deposit-feeding *Arenicola marina* or surface deposit-feeding *Nereis diversicolor* were added to organic matter poor sandy sediments, although both polychaetes stimulated overall benthic metabolism, they inhibited rates of sulfate reduction by 66 and 42% respectively, and there was an overall net re-oxidation of reduced sulfur pools in the in sediments by comparison with control mesocosms (Banta *et al.*, 1999). However, a minor addition of labile organic matter (dried yeast) equivalent to increasing the sediment organic matter pool from 0.06 to 0.08% dry weight, was sufficient to negate the oxidative effect of *N. diversicolor*, although *A. marina* still inhibited sulfate reduction by 85% with respect to similarly organically enriched control sediments (Banta *et al.*, 1999). Whereas, in a study of sulfate reduction in the wall sediments of natural burrows of the suspension-feeding soft-shell clam, *Mya arenaria*, although sulfate reduction rates were higher than in the bulk sediments, pools of reduced iron and sulfur compounds were lower, demonstrating that re-oxidation rates were also stimulated in the burrow wall sediments (Hansen *et al.*, 1996).

An indirect means of assessing the significance of anaerobic respiration processes and the balance between reduction and oxidation processes, is the determination of the benthic respiratory quotient (BRQ) from sediment-water column oxygen and inorganic carbon fluxes. The BRQ is the ratio between rates of sediment dark CO_2 production (total carbon oxidation rates) and sediment oxygen uptake, which integrates aerobic respiration and, the bacterial and chemical oxygen demands for the oxidation of reduced species generated by anaerobic bacterial metabolism. Theoretically, under balanced conditions, where all organic matter is either oxidised aerobically or any products of anaerobic mineralisation are completely re-oxidised, the CRQ value would be in the range 0.7–1.0 depending upon the composition of the organic matter mineralised (Andersen and Kristensen, 1988), although significant rates of nitrification (ammonium oxidation) can result in slightly lower values. Whereas, values substantially greater than unity indicate that there is incomplete re-oxidation of the end products of anaerobic respiration, which consequently accumulate in the sediment causing decreases in sediment redox status.

Unfortunately, the few studies from which it is possible to calculate BRQ, have focussed almost exclusively on species of polychaete worms (see Tab. II). Even within this confined group, it is difficult to observe any consistent effects, with the BRQ's of test microcosms

TABLE II Influence of Benthic Macrofauna on Sediment Oxygen and CO_2 Fluxes and Respiratory Quotients (RQ) Determined in Laboratory Microcosm Experiments. Feeding Group Abbreviations: SF, Suspension Feeder; SDF, Surface Deposit Feeder; SSDF, Sub-surface Deposit Feeder.

Organism/control	*Feeding group*	*O_2-flux (mmol $m^{-2}\,h^{-1}$)*	*CO_2-flux (mmol $m^{-2}\,h^{-1}$)*	*RQ*	*References*
Control		−0.38	0.80	2.1	Andersen and Kristensen, 1988
C. volutator	SDF/SF	−0.54	0.90	1.7	Andersen and Kristensen, 1988
N. virens	SDF	−1.14	1.63	1.4	Andersen and Kristensen, 1988
Hydrobia spp.	SDF	−0.61	1.02	2.0	Andersen and Kristensen, 1988
Control		−1.17	1.71	1.5	Banta *et al.*, 1999
N. diversicolor	SDF/SF	−2.45	3.86	1.6	Banta *et al.*, 1999
A. marina	SSDF	−5.02	6.45	1.3	Banta *et al.*, 1999
Control*		−2.48	3.60	1.5	Banta *et al.*, 1999
*N. diverscolor**	SDF/SF	−4.29	4.96	1.2	Banta *et al.*, 1999
*A. marina**	SSDF	−6.26	9.88	1.6	Banta *et al.*, 1999
Control 4 °C		−0.63	0.50	0.8	Kristensen *et al.*, 1992
Control 8 °C		−0.75	0.88	1.2	Kristensen *et al.*, 1992
Control 16 °C		−1.27	1.35	1.1	Kristensen *et al.*, 1992
N. Diversicolor 4 °C	SDF/SF	−0.79	0.65	0.8	Kristensen *et al.*, 1992
N. Diversicolor 8 °C	SDF/SF	−1.01	1.14	1.1	Kristensen *et al.*, 1992
N. Diversicolor 16 °C	SDF/SF	−1.27	1.96	1.5	Kristensen *et al.*, 1992

*Sediments supplemented with 0.06% particulate organic matter as dried yeast biomass.

sometimes yielding higher and sometimes lower values than the control microcosms. This limited data set also indicates as would be expected that other factors such temperature and sediment organic matter content also influence the effect of the macrofauna on benthic metabolism and sediment redox conditions.

Whilst overall it is not possible to draw any definite conclusions on the influence of the benthic macrofauna on specific anaerobic processes or the overall balance between aerobic and anaerobic metabolisms due to the paucity and somewhat contradictory nature of the available data, especially with respect to organisms other than polychaetes, intuitively some generalisations can be made founded on the relative influences of the different functional and taxonomical groups on oxygen and organic matter fluxes. On this basis, one would expect that sub-surface deposit feeders, inhabiting unlined burrows would most favour aerobic processes and oxidised sediment conditions, as they have little or no influence on organic matter inputs to the sediment, but enhance oxygen transfer to the sediment through burrow irrigation and stimulate sediment re-oxidation by transporting reduced deep sediments to the sediment surface as faecal castings during feeding. Similarly, surface deposit-feeding polychaetes and crustaceans may favour sediment oxidation by increasing oxygen fluxes without significantly affecting organic matter inputs, but to a lesser extent than sub-surface deposit feeders, due to the generally lower bioturbative activity of surface deposit feeders. In contrast, suspension feeders stimulate overall sediment metabolism through the biodeposition of organic matter and may stimulate anaerobic metabolisms to a greater extent than aerobic metabolism causing an increase in BRQ and a consequent reduction in sediment redox status. However, the degree of this potentially reductive effect will vary between species dependent upon their behaviour, and particularly on their relative influences on organic matter and oxygen fluxes to the sediment. Therefore, one would expect that suspension-feeding polychaetes and crustacean species inhabiting unlined burrows would have the least reductive effect, as they would have the greatest influence on oxygen transfer to the sediment and preferentially stimulate aerobic metabolism. Whereas, epifaunal suspension feeders would have the greatest effect as they stimulate organic matter inputs to the sediment, but have little or no influence on oxygen transfer and would consequently preferentially stimulate anaerobic metabolism and sediment reduction. Indeed, the presence of epifauna at the sediment surface may physically inhibit oxygen fluxes by reducing the surface area available for diffusive exchanges. Between these two extremes, infaunal bivalves would be expected to have intermediate impacts as their shells and siphons form complete or partial barriers to oxygen exchange with the sediment.

However, although such generalisations can be made on the potential effects of the diverse macrofaunal groups on the balance between aerobic and anaerobic metabolisms, there is a need for specific studies in order to quantify these effects and the role of contributing factors, such as temperature, sediment type, seston availability, local hydrodynamics and potential synergistic interactions between different components of the benthic community.

5 CONCLUSIONS AND FUTURE PERSPECTIVES

Whilst, from the numerous studies conducted on the influence of benthic macrofaunal populations, their physiological activity and comportment clearly demonstrate that they play potentially important roles in regulating organic matter turnover, nutrient cycling and exchange processes for oxygen, organic and inorganic dissolved nutrients between the sediment compartment and water column. It is difficult to extrapolate these data to field situations or to incorporate macrofaunal effects into sediment biogeochemical models. These difficulties are largely due to the fact that most experimental studies have been conducted in relatively short-term laboratory microcosm/mesocosm experiments to which populations of individual species were added or not, to defaunated and often homogenised sediments, rather than studies of natural mixed communities. This problem is further compounded by the fact that these experiments have also largely employed burrow forming polychaetes and to a lesser extent bivalves, and small sized crustaceans (almost exclusively *Corophium* spp.) as test organisms. Thus, to a large degree, even the potential influences of most benthic organisms remain poorly or completely unstudied.

This type of experimental design leads to two principal problems which limit the extrapolation of the data to natural systems. Firstly, the experimental simulations to a large extent mimic the short-term effects of macrofaunal colonisation events rather than those of metastable natural communities which may persist albeit with some degree of variation in biomass and taxonomic composition over long time periods. Therefore, the experimental mesocosms represent a non-steady state situation, whereas although natural communities may show seasonal and inter-annual variability, they may be considered as near steady state systems over long time periods. Such non-steady state dynamics can be clearly seen in the effects of the animal introductions on the fluxes of porewater nutrients and dissolved inorganic carbon to the water column (Kristensen and Blackburn, 1987; Hansen and Blackburn, 1992; Hansen and Kristensen, 1997; Nizzoli and Welsh, 1999; Banta *et al.*, 1999). The initial excavation of new burrows and the irrigation of these burrows by the animals causes a rapid flushing of porewater nutrients to the water column, resulting in a pulse of high nutrient fluxes over periods of a few hours or days, until the porewater nutrient pools are depleted and a new equilibrium is established between nutrient regeneration rates and fluxes. Thereafter, further slower changes in sediment water column fluxes of individual nutrients would be expected to occur due to changes in source-sink relationships as bacterial populations colonise new niches in the burrow walls. Whilst, establishment of bacterial populations could be rapid in many cases, in others involving organisms such as chemoautotrophic nitrifying bacteria which have minimum generation times of in the order of 24 hours (Kaplan, 1983), colonisation would be a prolonged process. For example in a microcosm study of the effects of sediment recolonisation by the neried worm, *Neries succinea*, after 3 days of incubation, denitrification rates based on water column nitrate were similar to those in intact sediment cores with similar densities of *N. succinea* (Nizzoli and Welsh, 1999) indicating that denitrifying bacteria had rapidly colonised the burrow wall sediments to levels similar to populations present in the "mature" burrows structures in field samples. Whereas, rates of coupled nitrification–denitrification where very much lower than in intact cores collected in the field and similar to those in the worm-free control mesocosms, indicating that there had been little colonisation of the burrow surfaces by slow growing nitrifying bacteria (Nizzoli and Welsh, 1999). Thus, it may take periods of weeks to months for source-sink relationships and flux changes related to them to stabilise.

However, even longer periods may be required before benthic metabolism stabilises. Mesocosm studies of the degradation of ^{14}C-labelled micro and macroalgal biomasses, indicate that there is little difference in the mineralisation rates of the labelled "fresh" organic matter in the presence or absence of macrofaunal populations and that the increase in overall benthic metabolism in mesocosms with animals is due almost exclusively to enhanced rates of mineralisation of "older" more refractory carbon pools already present in the sediment (Andersen and Kristensen, 1992; Kristensen *et al.*, 1992). However, since these more refractory pools of organic carbon are finite, the stimulation of benthic metabolism resulting from their mineralisation must by definition be a pulse event, even if the large pools of refractractory material present in most sediments may allow this pulse to be maintained for periods of months or years. Thus, in natural environments with persistent macrofaunal communities such pools of refractory organic matter may be largely exhausted. Indeed, under steady state conditions or over extended time periods, macrofaunal communities could only sustain higher rates of benthic metabolism by either augmenting organic matter inputs to the sediment or by decreasing carbon burial rates *i.e.* any increase in output (carbon oxidation + burial) can only be balanced by a corresponding increase in organic matter input to the sediment. Although suspension feeders, which enhance organic matter inputs to the sediment could sustain higher rates of benthic metabolism in the long-term, this would not apply to surface and sub-surface deposit feeders which have little influence on organic matter inputs to the sediment. Yet most of the micro- and mesocosm studies reporting macrofaunal enhancement of benthic metabolism have employed surface and sub-surface deposit-feeding organisms (see Kristensen, 2000, for data compilation). In these cases, higher rates of benthic metabolism could only be supported by lower rates of carbon burial.

Whilst, the presence of macrofaunal populations may very well reduce rates of carbon burial by stimulating mineralisation of more recalcitrant organic compounds, such as photosynthetic pigments, lipids, fatty acids and complex polymers such as lignin. This would result in only a minor stimulation of overall benthic metabolism, as generally only a few percent of the organic carbon input to marine sediments is buried (see Hedges and Keil, 1995, for review). Thus, the large differences in benthic metabolism observed between mesocosms with and without macrofauna cannot be due to changes in carbon burial rates. Since for example, to support the average, circa 2-fold difference in benthic metabolism reported between with and without macrofauna mesocosms (See Kristensen, 2000), would require a carbon burial efficiency of ~50% in the defaunated, control treatments, even if one assumed a zero burial rate in the animal treatments.

The second major difficulty in interpreting the largely laboratory derived data on macrofaunal influences on benthic metabolism and nutrient regeneration rates, is that not only has a limited taxonomic range of macrofauna been studied, but these species have been studied almost exclusively in isolation, as single species additions. In contrast, natural benthic communities are composed of taxonomically and functionally diverse mixtures. This again leads to problems in relating laboratory experiments to field conditions or in incorporating macrofaunal effects into sediment biogeochemical models. Since, through synergistic effects, the influence of a natural macrofaunal community is likely to be very different from the sum of its parts, even if data on the individual species composing the community were available to be summed.

If for example we consider populations of a surface deposit feeding polychaete, a bivalve suspension feeder and a mixed population of the same two species, with respect to how they influence organic matter inputs to and organic matter distributions within the sediment. The surface deposit feeder would cause little change in organic matter inputs, but mixes the organic matter deposited naturally onto the sediment surface into the deeper sediment strata. The suspension-feeding bivalve would augment organic matter inputs by actively filtering organic particles from the water column and depositing them at the sediment surface as

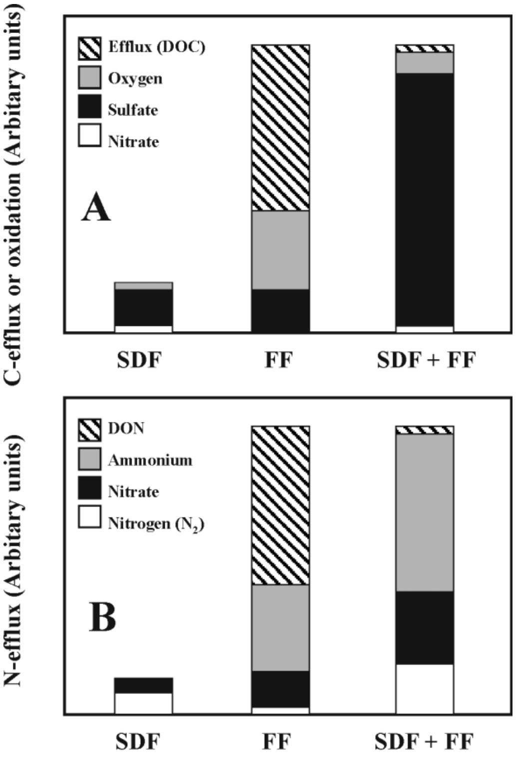

FIGURE 4 Idealised representations of the influence of a surface deposit feeder (SDF), a filter feeder (FF) and the combination of the same surface deposit feeder and filter feeder (SDF + FF) on: **A**. Organic matter mineralisation. Dissolved organic carbon (DOC) produced by hydrolysis of the sediment particulate organic matter either effluxes from the sediment or is oxidised using oxygen, sulfate or nitrate as respiratory electron acceptor. **B**. Effluxes of nitrogen mineralisation products to the water column. Hydrolysis of sediment particulate organic nitrogen generates dissolved organic nitrogen (DON) which either effluxes to the water column or is ammonified, the produced ammonium can again either efflux or be oxidised to nitrate via nitrification and this nitrate in turn can efflux to the water column or be denitrified and escape the sediment as N_2 gas. The predictions are based on the organisms effects on organic matter inputs and distribution in the sediment and the biogeochemical models of Blackburn and Blackburn, 1996a,b,c and Blackburn, 1996 (see section 2.3). In these scenarios, the SDF alone does not augment organic matter inputs but mixes organic matter into the sediment, the filter feeder increases organic matter inputs but causes little mixing and in combination, the filter feeder augments deposition of organic matter onto the sediment surface and the surface deposit feeder transports this organic matter to the deeper sediment strata. Thus, these situations roughly correspond with the low mixed input, high top input and high mixed input situations in Blackburn's models.

faeces and pseudofaeces, but being relatively sessile would cause little mixing of the deposited material into the sub-surface sediments. Whereas, in combination the suspension feeder would increase organic matter biodeposition to the sediment surface and the surface deposit feeder would ingest and redistribute this material into the deeper sediments. Thus, broadly speaking these situations would correspond to the low mixed input, high surface input and high mixed input scenarios in the biogeochemical models of Blackburn and his colleagues (Blackburn and Blackburn, 1993a,b,c; Blackburn, 1996). The model predictions of these three scenarios in terms of carbon metabolism and nitrogen regeneration are graphically summarised in Figure 4. Whilst, this comparison should be considered as a very rough approximation, as other macrofaunal effects such as increased influxes of bacterial respiratory substrates such as oxygen and nitrate from the water column and enhanced effluxes of porewater substrates to the water column, are not included in the models. It clearly demonstrates that neither quantitatively nor qualitatively are the effects of the two organisms the sum of those of the individual animals and that the combination of the two animal populations causes major shifts in the pathways of organic matter mineralisation and the speciation of the mineralisation products which are returned to the water column.

Thus, in conclusion the greatest need at present is for field studies to quantify the true influences of natural, mixed macrofaunal communities on benthic metabolism, organic matter turnover, organic matter burial and nutrient regeneration rates, to provide the basis for the inclusion of macrofaunal community function in biogeochemical models. Unfortunately, this aim will not be easy to achieve and will require the development of new approaches to allow the quantitative evaluation of the *in situ* influences of the benthic macrofaunal community on sediment biogeochemistry.

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