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Sandy sediments as active biogeochemical reactors: compound cycling in the fast lane

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ABSTRACT: The concept of assessing benthic biogeochemical standing stocks as an ecologically relevant parameter has been challenged by one of a dynamic nature: in sands, low standing stocks may mean low carbon burial efficiency due to rapid turnover aided by advective interfacial flows. This concept suggests that a large, diverse and very adaptable population of microbes is present in sands, and that these have a previously unforeseen biogeochemical importance. This view has profound consequences for the scientific outlook on the ecological role of permeable sediments and on the methodological strategies used in the study of coastal ecosystems. Based on a review of the current literature and results gathered at a coastal setting, progress within this new paradigm is examined and underlying questions are speculated upon. The evidence so far shows that, in permeable sediments and at timescales of seconds to a few hours, the dynamics of advective flow to a large extent control microbial diversity, the rates of microbial processes, the size of organic and inorganic pools, and even their respective changes. The importance of obtaining further information on the microbial diversity, the structure of different communities present in sands and their link to biogeochemical function arises from recent field studies. What is also clear from the available evidence is that only a combination of different techniques and approaches, some of which are under development on the fringes of previously almost water-tight research areas, will further understanding of the important functional role of microbial populations in benthic ecosystems.

KEY WORDS: Permeable sediments · Sand · Biogeochemistry · Carbon cycling · Coastal zones · Shelf zones

INTRODUCTION

Coastal shelf seas as biogeochemical hotspots

The flow of carbon and nitrogen from land to sea is largely intercepted by benthic microbial communities in coastal sediments. Hence, the coastal ecotone is a transport-reaction node, one that modulates elemental fluxes between continental ecosystems, including human settlements, the sea and the atmosphere (e.g. Rabouille et al. 2001, Middelburg et al. 2005). Observable effects of this functional role include support for higher rates of primary production in coastal waters. These are promoted by higher nutrient availability (Mackenzie et al. 2002), on the one hand introduced by river discharge, diffuse sources and benthic remineralization, and, on the other hand, by upwelling water masses which deliver remineralized inorganic solutes produced by the breakdown of organic compounds settled in the continental slope and deep sea. Consequently, 30 % of the total anthropogenic CO_2 ($118 \pm 19 \times 10^{15}$ g C) sunk into the ocean via the biological pump is found over the continental shelves (depth <200 m), and 50 % above the 400 m isobath (Sabine et al. 2004). An important consequence of the combination of shallow depths with all the intersecting POC and PON transport pathways is that the efficiency of carbon transfer into underlying sediments is higher. Accordingly, the conti-

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nental shelf is an important burial ground for organic matter, with >90 % ($>1 \times 10^{14}$ g C yr^{-1}) of the global suspended load being buried there (Hedges & Keil 1995). In addition, larger photic zone to water column depth ratios make the journey of fresh POM into the sediment a shorter one, thus guaranteeing that mineralization substrates arrive at the sediment–water interface in a very fresh and labile condition.

Paradigm shift

The importance of the continental fringe and shelf in the global carbon cycle cannot be overemphasized, particularly since the coastal zone will bear the brunt of human occupation and climate-related changes for decades to come (e.g. Crossland et al. 2005). However, while recognizing the importance of shallow-water carbon and nutrient recycling in the global budget, the marine scientific community has nurtured a longstanding paradigm, one arising from the observation that high benthic (re)mineralization rates were directly correlated to organic matter content. This observation somehow reinforced the notion that the size of the benthic organic pool determined the functional importance of coastal sediments. The failure to effectively test the previously mentioned correlation for causation, mainly due to methodological constraints, led to the widely accepted, but misguided, view whereby low or residual organic content of sediment beds was a consequence of their low biogeochemical importance.

However, the effectual cause for the observed correlation was the zeroth-order kinetics of aerobic mineralization: with increasing standing stocks, the breakdown of organic matter would only be dependent on oxidant exposure time and not directly on carbon loading. Hence, when carbon loads are significant and solute transport is physically limited (i.e. by diffusion at the Diffusive Boundary Layer), hindering the supply of oxygen and other terminal electron acceptors from the water column to the sediment, a fraction of the loaded carbon might escape mineralization and be preserved by burial (Betts & Holland 1991). Because shorter exposure time to oxidants, and oxygen in particular, leads to higher carbon burial efficiency (Hartnett et al. 1998), higher accretion rates will shorten the exposure of organics to oxidants under transport-limited conditions and thus increase carbon burial.

The role oxygen plays in carbon preservation has been intensely debated because oxygen is the primary electron acceptor for organic matter decomposition and it has been well established that oxygen-deficient zones are sites of high carbon burial efficiency (Hartnett & Devol 2003). The link between organic content and biogeochemical importance was further stressed by the higher sediment–water interface concentration gradients found at muddy sites, which led to larger cross-interface fluxes as calculated by Fick's first law when compared with sandy sediments: under steady-state conditions, high fluxes balanced high reaction rates, so a large organic pool equated large biogeochemical reaction rates. What got lost in translation to a large section of the scientific community was that the reverse was not necessarily true. The traditional concept of a passive sediment bed, e.g. one receiving the input of settling organic matter and inorganic particles, subsequently buried by continuous accretion and mixing by infauna, was thus strengthened.

Sands, with an organic content 1 to 2 orders of magnitude lower and primarily consisting of low surface area particles compared to muds, apparently provide fewer possibilities for microbe attachment and consequently became (unsurprisingly) a bleak field of study for the biogeochemist and the microbial ecologist. The association between the burial efficiency of organic carbon, mineralization rates and the surface area of sediment particles was not to undermine traditional views until the seminal paper of Riedl et al. (1972) suggested that the entire volume of the ocean could be filtered through permeable sediment beds of coastal ecosystems in just 14 000 yr.

Sands are permeable, thus permitting water to flow through the interstitial space when horizontal pressure gradients are present (Darcy 1856). Apart from hydraulic effects, gradients can arise from wave effects (Webb & Theodor 1968, Rutgers van der Loeff 1981, Shum 1992), intersection of obstacles by boundary layer flow (Thibodeaux & Boyle 1987), oscillating or rotational flow (Huettel & Gust 1992) and density driven convection (Webster et al. 1996, Rocha 2000). Irrespective of the driving force, advective mass transfer seriously questioned the traditional view of the passive sediment bed. Contrary to the previous ethos, the low standing stocks of organic matter and inorganic mineralization by-products characteristic of permeable sediments might not, after all, reflect low biogeochemical importance. Instead, the relative organic poverty of sands could be due to rapid turnover. Experimental studies showing advective transport of oxygen into permeable beds (Booij et al. 1991, Ziebis et al. 1996), flow induced trapping of particulates by sand (Huettel et al. 1996, Rusch et al. 2001), and rapid removal of decomposition products (Huettel et al. 1998, Rocha 1998), all supported the hypothesis whereupon permeable sediments are sites of accelerated organic matter turnover (Boudreau et al. 2001, Huettel & Webster 2001).

The global relevance of this maturing paradigm is related to the large areal cover of sands on continental shelves worldwide (Emery 1968). The concept of assessing benthic standing stocks as relevant when rating the functional importance of different sediment beds was thus challenged by one of a dynamic nature: low standing stocks could just mean low burial efficiency (large mass fluxes of oxidants and metabolites ⇒ high microbial activity ⇒ high turnover rates [mineralization] ⇒ low residence time), suggesting that a large, diverse and very adaptable population of microbes could be present in sands and that these would have a previously unforeseen biogeochemical importance. This view would have profound consequences on (1) the scientific interest in the biogeochemical, functional role of permeable sediments, and (2) the methodological strategies used in the study of coastal ecosystems.

COASTAL SANDS AS BIOCATALYTIC FILTERS

Overcoming methodological constraints

The new paradigm suggests that most continental shelf sands constitute sites of enhanced organic carbon turnover and may act as 'biocatalytic filters' (Precht & Huettel 2003) along the transport route linking continental ecosystems to the deep sea. By estimating that interfacial advection might drive one-third of the global benthic flux of oxygen and more than half of the phosphate flux, Meile & Van Cappellen (2003) convincingly showed that enhanced solute transport may significantly enhance benthic–pelagic coupling worldwide. So far, the real magnitude of this enhancement is not measurable. Even though early flume studies demonstrated that advection of porewaters in permeable sediments supports complex 2- and 3-dimensional spatial and temporal biogeochemical zonation of the sandy seafloor (Forster et al. 1996, Ziebis et al. 1996, Huettel et al. 1998), in fact, the experimental characterization of solute transport and supporting reaction rates in sandy sediments is deterred by several obstacles: firstly, the pressure-induced flow pattern is 3-dimensional, while reaction rates and particle and solute concentrations are mainly quantified by point measurements; secondly, techniques employed to obtain point measurements are usually intrusive in nature, thus disturbing the flow pattern to some degree; and finally, the pressure fields driving interfacial flows are highly dynamic and vary dramatically over short timescales depending on currents, waves and topography disturbing the local water flow. Accordingly, obtaining representative measurements under different conditions that combine all possible forcing functions is in effect not feasible with the present degree of knowledge.

Because advective interfacial flow controls the supply and removal of solutes and particulates in sands, the classical coring approach to quantify flux-defining concentration gradients, or the use of enclosed chamber techniques (Tengberg et al. 1995) are clearly inadequate to resolve fluxes coupling benthic reactivity and pelagic processes. Also, cutting off porewater flow by encasing sediment samples in cores or slurries to study reaction kinetics in the laboratory would hinder ongoing microbial reactions that relied on advective loading of metabolites. A new sampling methodology, one inclusive of the dynamic nature of interfacial advective flow, had to be developed.

Benthic flux chamber studies (Booij et al. 1991, Huettel & Gust 1992) are a case in point. Glud et al. (1996a) showed how fluxes measured using enclosed chambers in permeable sediments (k [permeability] $> 2 \times 10^{-12}$ m^2) were dependent on stirrer-induced radial pressure gradients developing at the sediment–water interface. Porewater flow regimes similar to those found under microtopography-intersecting boundary layer flows were formed across the chamber as a consequence of centrifugal effects. Inasmuch as the study by Glud et al. (1996a) aimed to constrain field conditions for the use of chambers in benthic landers, it also showed that the porewater flow patterns created by chamber design and stirring rate could be predictable (Basu & Khalili 1999). Flux chambers designed with this in mind were then deployed to study the influence of pre-defined advection regimes on total oxygen uptake in coarse sediments of the German Bight (Janssen et al. 2005a). For 3 different sites with contrasting grain sizes, the study by Janssen et al. (2005b) demonstrated that an advective regime imposed on the seabed promoted a ~30% increase in the benthic metabolic rate, compared to control experiments without a pressure field.

Nonetheless, quantifying flux magnitudes and assessing microbial metabolism in natural settings depends on the extent of local interstitial circulation patterns, which could be co-driven by wave motion. Modeling studies demonstrated how, apart from being able to translate orbital motion to the porewater (Shum 1992), waves might also promote longitudinal oxygen gradients of the same order of magnitude as the vertical gradients measured in natural settings (Shum 1993). Even at low energy settings (waves 10 cm high) porewater velocities in shallow ripple fields, as measured *in situ* using fluorescent tracers (Precht & Huettel 2004), demonstrated that advective transport through the sediment–water interface exceeded molecular diffusion by 3 orders of magnitude. In addition, wave tank studies (Precht & Huettel 2003) showed that, under the combined effect of waves and unidirectional flow, ripple migration will promote dislocation of the porewater flow fields down current. This evidence is important in the context of benthic biogeochemical metabolism. Because benthic mineralization is enhanced by repetitive oscillation of the redox boundary (Sun et al. 2002), translational movement of the oxic/ anoxic boundary due to ripple migration would expose organic matter to alternating redox conditions, thus promoting its degradation. Supporting the notion that metabolic rate distribution moved along with the ripple field, the 2-dimensional pattern of oxygen distribution as measured by planar optodes (Glud et al. 1996b, 2001) was shown to trail flow fields generated by migrating ripples (Precht et al. 2004). Anoxic upwelling zones under ripple crests were shown to alternate with oxygen-rich downwelling areas beneath ripple troughs. So formed, the redox field moved upcurrent with the migrating ripples, much like a conveyor belt. The intensity of this effect was dependent on the speed of ripple migration and on the sediment permeability. Above a threshold velocity and for a fixed permeability, instead of moving alternating redox boundaries, migrating ripples create a continuous oxidized layer, hence hindering the transfer of reduced solutes into the overlying water.

On the other hand, while experiments designed to isolate the forces driving porewater motion promote the understanding of the governing principles behind interfacial advection and its underlying role on the biogeochemistry of sands, they also illustrate the challenge of quantifying sediment–water fluxes under natural conditions. For instance, flux measurements over a rippled seabed need to be integrated over whole inflow and outflow areas along sampled sections of the seafloor. So far, the best candidate to fulfill this role is the eddy-correlation technique (Berg et al. 2003). This non-invasive method relies on contemporary measurements of fluctuating vertical velocities and rapidly changing oxygen concentrations within the measuring volume of an acoustic Doppler velocimeter by using a fast-response microsensor. While field testing of the method concentrated on oxygen as the target species (Berg et al. 2007, McGinnis et al. 2008), the procedure could be applied for any solute, as long as the response of the chemical sensor is able to discriminate concentration changes due to turbulent motion. Whilst the method is rapidly evolving into the standard for quantifying solute fluxes in dynamic aquatic environments, effective coupling between the measured fluxes and benthic reaction in porewater flow fields is far from being attained. The 2 main obstacles to progress in this direction that have persisted so far are the lack of (1) measurable constraints on the magnitude of flow penetration into a given sandy substrate, and (2) convincing *in situ* measurements of solute concentrations and reaction rates, coupled to the local flow field, supporting laboratory demonstrations.

Permeability is usually measured as a bulk sediment property under unidirectional flow. In reality it is a tensor, which means that its magnitude changes along the 3 orthogonal axes of space. While most of the experiments dealing with advective flow in laboratories have worked with sorted sands and the relevant modeling is based on the assumption of isotropic media, consolidated natural sediments are not characterized by these simplified conditions. Because flow within the porous matrix is conditioned by the magnitude of the permeability vector along the 3 directions, one of the most obvious shortcomings of research to date is the incapability of introducing this behaviour into observations and subsequent data analysis. For instance, consider the 2-dimensional permeability anisotropy — that is, k_z/k_x, the ratio between vertical and horizontal permeability — as determined *in situ* for the first time on a natural ripple field on the Ria Formosa coastal lagoon, Southern Portugal (Fig. 1), using a methodology yielding high-resolution vertical (k_z) and horizontal (k_x) permeability gradients (Rocha et al. 2005). The analysis shows that clear preferential flow pathways (vertical permeability dominant over horizontal on the trough and crest; Fig. 1, inset A), similar to that predicted by laboratory experiments, would develop under Bernoulli pressure gradients because the direction of the permeability vector determines the flow path (Darcy 1856). Although the sediment used in this experiment was coarse overall (median grain size 370 µm, bulk $k = 1$ to 6×10^{-11} m^2 at a vertical scale length of 10 cm), smaller-scale spatial inhomogeneities effectively restricted the potential for fluid motion through the sediment pores to the superficial 1 cm layer (Fig. 1, inset B, where below 1 cm depth, horizontal direction of the permeability vector is dominant, thus impeding vertical flows irrespective of pressure gradient). In this case study, mixing of particles and solute reactants could occur to ca. 5 cm depth on the left-hand side ripple (Fig. 1, inset A), but would not exceed the upper 1 cm layer on the right-hand side ripple (Fig. 1, inset B). This method not only reveals the large variability in permeability over small spatial scales in natural settings, but also provides clear evidence on the natural constraints to the filtering capacity of sandy sediments, required to adequately assess the global importance of the permeable seabed in organic carbon mineralization. Implications for the quantification of supported benthic reaction rates are obvious: sub-samples of sediment taken from field sites have to be subject to flow, with specific flow rates based on *in situ* measurements, and the natural constraints to the pore velocity presented by the natural permeability will eventually modulate derived reaction kinetics. Techniques such as those put forward by Polerecky et al. (2005), where oxygen consumption rates are measured by the stepwise insertion of microsensors in natural cores permeated by externally impressed flow, as well as the use of flow-through reactors to derive stoichiometric models of biogeochemical reactions and pathways (Laverman et al. 2006 and references therein) should become the standard for microbial reaction rate measurements in the laboratory.

Reconciling laboratory studies with field studies

Whilst field and laboratory studies are crucial in defining the role of interfacial exchange processes on the biogeochemical function of permeable sediments, prognostic capability will only be available when models reproducing the empirical data are developed. To date, modeling has provided important aides to research by assisting in the visualization of flow patterns that are difficult to reproduce in the laboratory (e.g. Meynsman et al. 2007), and also in the study of arrays of point measurements in field settings. While understanding of the governing principles and mapping of potentially active sediments advances (Forster et al. 2003), and technical bottlenecks for field-based quantitative research are overcome (see above), the modeling of porewater advection per se, as well as predicting its impact on the local or global geochemical cycles, remains a difficult task (Elliot & Brooks 1997a,b, Packman & Bencala 2000). Recent studies (Cardenas & Wilson 2007a,b) investigated temporal coupling between turbulent water columns and topography-driven flow in permeable sediments, including composite flow arising from the presence of submarine groundwater discharge, using sequentially coupled numerical formulations. The 2-dimensional simulations suggest that interfacial flow patterns and boundary layer flow are correlated through water column eddies, which supports the use of the eddy-correlation technique (Berg et al. 2003) in coupling interfacial exchange to benthic reaction.

Nonetheless, models need to reconcile data describing the patterns of flow as well as concentration fields of target compounds, including relevant biogeochemistry. This perception can be illustrated by considering the distribution of chl *a* in a natural ripple field, sampled perpendicularly to the ripple development in a coastal setting. The data presented in Fig. 2 show that chl *a* accumulates in the inflow and outflow areas of the ripple sequence, as postulated by theoretical and flume studies (Huettel et al. 1996, Precht & Huettel 2003). In addition, the local flow pattern, calculated based on the knowledge of permeability microgradients (Rocha et al. 2005) and the pressure gradient at the interface (Elliot & Brooks 1997a, Precht & Huettel 2003), justifies this observation easily. This simple visual correlation shows that, although the local hydrodynamics may prevent passive settling of pelagic microalgae, the inflows created by Bernoulli effects promote loading of carbon into the sediment. In addition, benthic primary production (note the chl *a* maxima in the outflow areas) may respond to rapid mineralization of newly buried organic matter. Thus, porewater flow pathways almost certainly link the supply of organic carbon to benthic primary production. Ripple migration will necessarily carry along some of the more recalcitrant particulates, as suggested by the presence of discrete concentrations ('blobs') of organic matter below the ripple line (left-hand side ripple). This effect may arguably create microbial microniches within migrating ripple fields, adding potential for the occurrence of heterotrophic denitrification, and may also extend the residence time of both active microalgae and less labile carbon within the sandy seafloor. For instance, Pilditch & Miller (2006) found similar results in the laboratory under controlled flow conditions and different ripple geometries. Results from their study suggest that the combination of hydrodynamics and bedform heterogeneity lead to ripple-scale patchiness of organic matter input into coastal shelf sediments, along both the vertical and horizontal directional axes. Conversely, Huettel et al. (2007) found that algal decomposition rates in percolated sands were far from explaining the turnover rate of algal cells found in natural bedforms, hence implying that part of the cells are just temporarily retained within the sediment bed.

These results demonstrate that various patterns of carbon loading are established in natural ripple fields in response to porewater flow, caused by the intersection of bedforms with boundary-layer currents. Even though passive settling of particulates may not be possible under local hydrodynamic conditions, an active mechanism of carbon burial is present over sandbeds. However, within the ripple beds themselves, a series of microniches, potentially capable of sustaining both bacterial metabolism of a very diverse and adaptable nature, can potentially develop along the interstitial flow paths (Ishii et al. 2004, Bühring et al. 2005, Musat et al. 2006). Interesting questions develop as a consequence: What is the role of sands in providing nutrients to pelagic production temporarily stuck in migrating ripples? How do these algal cells benefit from the active biogeochemical environment — and conversely, how do they affect it? What is the feedback into the biological pump? How does this temporary burial affect microbial diversity and how does the latter correlate with different mixing regimes? With respect to the latter, Bühring et al. (2005) found different vertical scales of bacterial fatty acid distribution according to grain size, which could be an indication that bacteria are mixed deeper into coarser sediments. However,

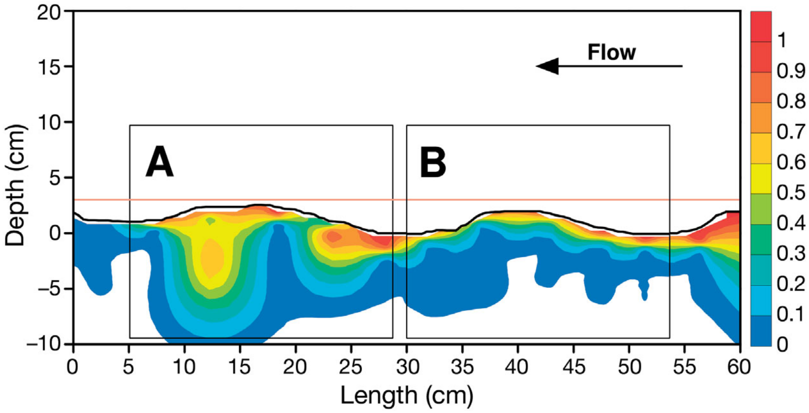

Fig. 1. Two-dimensional mapping of the microscale permeability anisotropy of a shallow sand ripple field in the Ria Formosa, Southern Portugal. Horizontal red line serves as reference relative to ripple height. Colour contours show the anisotropy as the ratio between local vertical permeability (k_z) and horizontal permeability (k_x). Kriging interpolation algorithm of 110 point measurements of k_x and k_z, aligned perpendicularly to ripple crests, with depth discrimination between 0.2 and 1.5 cm, with greater resolution near the sediment–water interface. A value of 1 indicates identical orthogonal components of the permeability vector, ensuing in a preferential flow pathway with an angle of 45° to the horizontal. Inset A: Local anisotropy field showing deep (>5 cm) potential flow pathways at ripple crest and trough, similar to sorted sand ripples used in flume experiments (Huettel et al. 1996, 1998, Ziebis et al. 1996). Inset B: Evidence of the natural spatial heterogeneity in preferential flow pathways. Note that, although inserted in the same ripple sequence as A, no available deep penetration capability is evident; instead, the permeable area is restricted to the ripple surface (<1 cm)

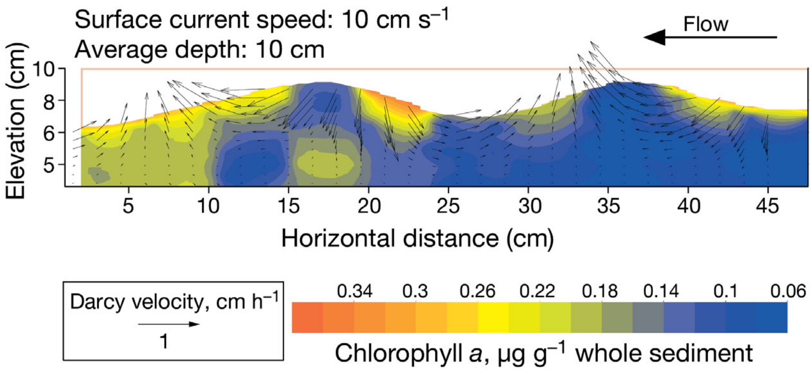

Fig. 2. Two-dimensional mapping of chl *a* distribution in a tidal ripple field in the Ria Formosa, sampled in December 2005. Superimposed is a 2-dimensional rendering of the Darcy flow vector field, calculated for an overlying water current speed of 10 cm s^{-1} and a depth of 10 cm. Colour contours represent the interpolation of 140 point measurements of benthic chl *a* extracted from whole sediment samples in 80 % acetone for 24 h in the dark at –20°C. Pigment concentrations determined according to Lorenzen & Jeffrey (1980). Orthogonal components of the pore flow field were calculated individually by application of Darcy's law using the respective permeability vector component, measured according to Rocha et al. (2005) at each of the 140 sampling points. The horizontal pressure gradient driving the flow at the interface was calculated according to Elliot & Brooks (1997a). For illustrative purposes, the 2 resulting orthogonal flow vector matrices where then summed on a point-by-point basis, thus rendering the plotted vector field. The flow magnitude is represented in a graphic depiction of a reference vector on the lower left (to scale)

these authors, and Musat et al. (2006) also found that fluorescent *in situ* hybridization indicated the presence of large populations of sulphate-reducing bacteria, which indicates either that sulphate reduction is possible in oxic environments (see de Beer et al. 2005 for concomitant sulphate reduction rates), or conversely, that patterns of flow are not directly deducible from an apparent correlation between grain size and bulk permeability (see Figs. 1 & 2). However, these findings beg the question of starvation/survival metabolism in benthic bacteria, and also suggest that our knowledge of the main biogeochemical reaction pathways in sands might be flawed, either because the relevant metabolic pathways are not known, or because benthic microbial diversity and structure is grossly underestimated. In addition, relevant issues develop with regard to the effects of particulate loading of sands on the flow pattern itself, because clogging, even temporary, will alter flow pathways by changing the permeability field. Our interpretation of interacting variables in sands is further complicated by the presence of bioturbating and bioirrigating infauna (Timmermann et al. 2006), which is sometimes present in large densities. While extension of flushing areas below the sediment–water interface seems to occur to a large extent (Volkenborn et al. 2007), the relative impact of the organisms themselves on the total flushing capacity of coastal shelf sands is largely unknown.

CONCLUSIONS

All evidence gathered so far shows that, in permeable sediments, it is the dynamics of advective flow that controls, to a large extent, microbial diversity and the rates of microbial processes (de Beer et al. 2005, Musat et al. 2006), the size of organic (Pilditch & Miller 2006, Huettel et al. 2007) and inorganic pools and even their changes (Ehrenhauss et al. 2004, Janssen et al. 2005b), at timescales of seconds to a few hours. However, it is painfully clear from a cursory review of the literature that many coastal studies tend (still) to overlook this simple fact. At lagoons and intertidal sites, in particular, 'one-off' sampling strategies (e.g. a couple of core profiles taken in the laboratory, eventually complemented by static incubations, with results being extrapolated for a whole season or sediment morphological type) are unfortunately quite common in coastal ecosystem studies. When not exercised with cautionary principles that depend on ensuing data usage, this methodology will, necessarily, lead to gross errors in the proper identification of solute distributions and ongoing microbial processes. Under these conditions, the quantification of interfacial fluxes and supporting process rates, as well as their subsequent extrapolation to carbon and nutrient budgets in nature, would be severely compromised. Considering the already complex problems facing the scientific community, pressured to fathom the role played by coastal zones as a carbon sink and the ecological consequences of nitrate enrichment (Vitousek et al. 1997, Codispoti et al. 2001, Hulth et al. 2005, Codispoti 2006), such procedures amount to 'Cargo Cult Science' (Feynman 1974). 'Data' from these approaches should therefore be evaluated with extreme care.

Apart from the ongoing development of very promising non-destructive techniques for the visualization of microbial processes as they occur and real-time measurements of process rates (Kühl 2008, this Special), it is clear that the microbial diversity of sands, as well as the different metabolic pathways possible in this environment, have only very recently begun to be studied, and a strong effort must be made in this area. It is crucial that further information on microbial diversity and community structures present in sands and their link to biogeochemical function is obtained. More so than the technical developments, however, it is the cross-disciplinary outlook that is effectively showing more promise in advancing the understanding of the important functional role played by microbial populations in permeable benthic ecosystems, and this approach should be strongly supported.

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