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Benthic Exchange and Biogeochemical Cycling in Permeable Sediments

Markus Huettel,¹ Peter Berg,² and Joel E. Kostka³

¹Department of Earth, Ocean, and Atmospheric Science, Florida State University, Tallahassee, Florida 32306-4320; email: mhuettel@fsu.edu

²Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904-4123; email: pb8n@virginia.edu

³Schools of Biology and Earth and Atmospheric Sciences, Georgia Institute of Technology, Atlanta, Georgia 30332-0230; email: joel.kostka@biology.gatech.edu

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Abstract

The sandy sediments that blanket the inner shelf are situated in a zone where nutrient input from land and strong mixing produce maximum primary production and tight coupling between water column and sedimentary processes. The high permeability of the shelf sands renders them susceptible to pressure gradients generated by hydrodynamic and biological forces that modulate spatial and temporal patterns of water circulation through these sediments. The resulting dynamic three-dimensional patterns of particle and solute distribution generate a broad spectrum of biogeochemical reaction zones that facilitate effective decomposition of the pelagic and benthic primary production products. The intricate coupling between the water column and sediment makes it challenging to quantify the production and decomposition processes and the resultant fluxes in permeable shelf sands. Recent technical developments have led to insights into the high biogeochemical and biological activity of these permeable sediments and their role in the global cycles of matter.

1. INTRODUCTION

Sediments composed of sand or gravel cover approximately 50% of the continental shelves and 4% of the ocean floor (Hall 2002) (Figure 1). One key characteristic that sets these sediments apart from the majority of the seafloor is their high permeability. Permeability denotes the resistance to flow of water through the sediment (Bear 1972); because marine sediments are composites of particles and water, they are all permeable to some degree. Permeability starts measurably influencing biogeochemical and biological processes in the surface layer of marine sediments when pressure gradients in the benthic environment can drive pore-water flows that transport solutes and small particles more effectively than Brownian molecular motion. Investigations using inert tracers (such as bromides, fluorescein, and microbeads) have indicated that, in natural marine sands,

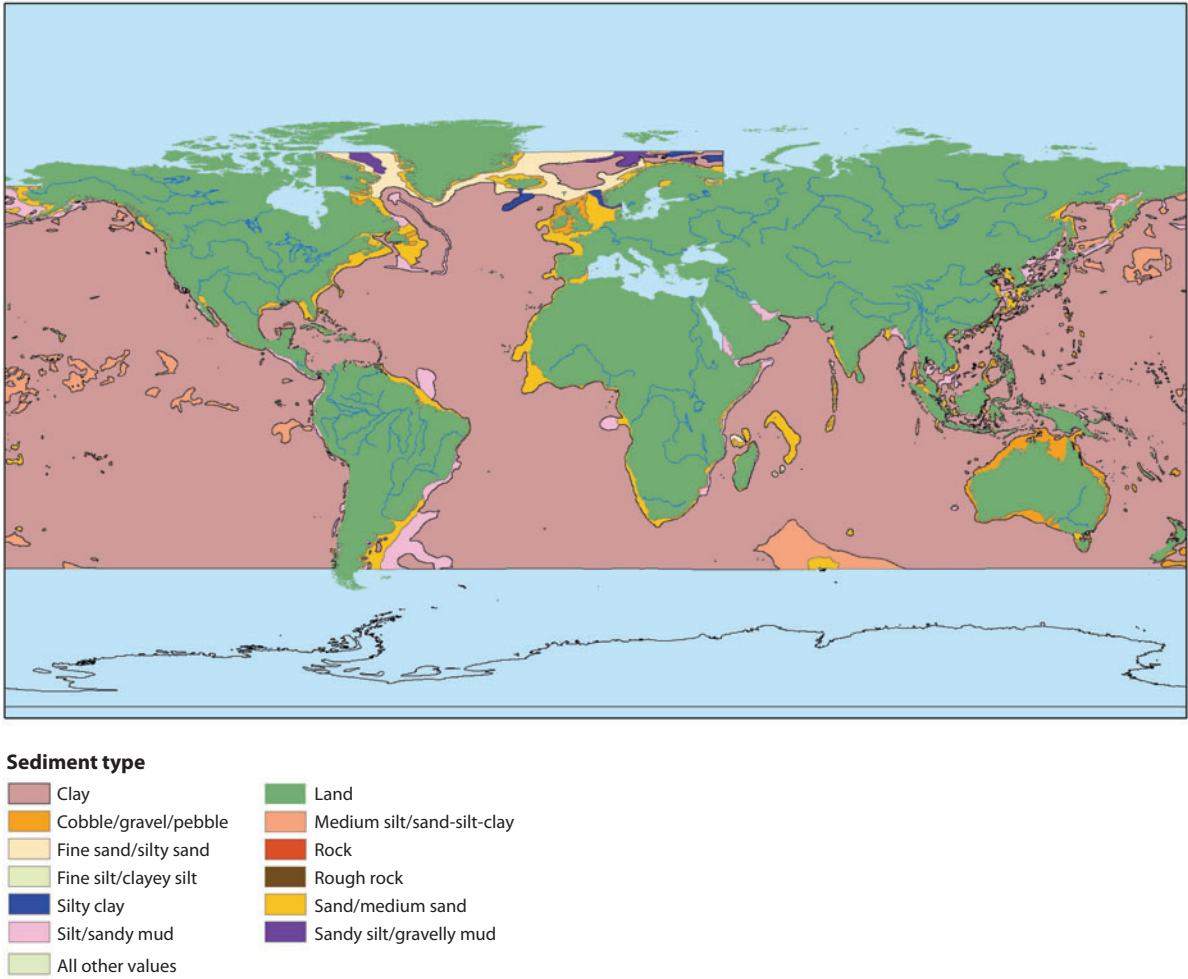


Figure 1

Distribution of sediment in the oceans. The yellow and orange areas skirting the coasts of the continents are areas dominated by sand or gravel and represent the areas with permeable sediments. Adapted from a sediment map posted by Arlene Guest of the Naval Postgraduate School's Department of Oceanography (<http://www.oc.nps.edu/~bird/oc2930/sediments>) based on High Frequency Environmental Acoustics (HFEVA) data from the Naval Oceanographic Office.

this threshold is reached when permeability exceeds 10^{-12} m^2 (Huettel & Rusch 2000, Huettel et al. 1996). In this review, we therefore define permeable sediments as those with a permeability greater than 10^{-12} m^2 ; when this threshold is reached, interfacial solute fluxes deviate significantly from those associated with molecular diffusive transport, and advective pore-water flows dominate exchange processes in the sediment surface layers. This fluid exchange tightly couples shelf water column and sedimentary biogeochemical processes.

In contrast to the deep ocean, where environmental conditions are relatively constant, on the continental shelves the proximity to land and decreasing water depth amplify physical, chemical, and biological processes affecting biogeochemistry and cycles of matter. The shallow depths in these areas limit the dilution of inorganic and organic nutrients reaching the coastal zone via the atmosphere, rivers, terrestrial runoff, and groundwater discharge, and the resulting nutrient gradients lead to intense primary production in shelf waters. Satellite maps reveal that the continents are bordered by a rim of increased chlorophyll concentrations that fluctuate on daily, seasonal, and yearly timescales (Jönsson et al. 2011), reflecting the dependency of shelf productivity on climate-related patterns, ocean circulation, and anthropogenic influences.

Approximately 20% of global pelagic primary production takes place on the shelf (Jahnke 2010), and because the average water depth of the shelf is only 65 m, a large fraction of the production can reach the seafloor, where benthic primary producers can add to the organic matter input to the sediment. Paradoxically, the sand beds that dominate the seafloor of the inner shelf are characterized by low standing stocks of organic carbon and dissolved reactants. This has led to interpretations that these sediments are biogeochemically relatively inactive and thus play an insignificant role in the coastal and global cycles of matter. In the past two decades, the deployment of novel in situ technologies, including benthic advection chambers (Janssen et al. 2005a), eddy correlation instruments (Berg et al. 2003), in situ mass spectrometers (Bell et al. 2012), planar optode landers (Glud 2008), and benthic observatories (Jahnke et al. 2008, Sansone et al. 2008), has revealed that these sands are biogeochemically highly active. These investigations suggested that the high permeability converts these sandy beds into biocatalytic filters that are notable for their high reaction rates, intense recycling, and extreme spatial and temporal dynamics of biological and geochemical processes.

Results from major research programs on the continental shelves of the eastern United States, western Europe, the East China Sea, and the Mediterranean Sea have consistently indicated that most of the biogenic particulate matter is remineralized on the shelves and that less than 5% of this material is exported to the adjacent slopes (Chen 2010). Globally, the shelf may be responsible for 90% of sedimentary mineralization (Gattuso et al. 1998), and permeable sands dominate these sediments. Their biocatalytic filtration activity contributes to the effective remineralization on the shelf and may partly explain why the organic matter dissolved in seawater or buried in deeper sediments bears little isotopic or chemical evidence of terrigenous origin, despite the magnitude of the land-derived carbon inputs to the coastal zone ($\sim 27 \text{ Tmol y}^{-1}$ for dissolved organic carbon, $\sim 18 \text{ Tmol y}^{-1}$ for particular organic carbon) (Chen 2010, Hedges et al. 1997).

This article reviews transport and reactions in shelf sands and highlights unique characteristics of these sediments. We show that the permeable shelf sands play a critical role in the functioning of the continental shelf as a biogeochemical filter at the land-sea boundary, and that this biocatalytic filter is increasingly threatened by anthropogenic activities.

2. PERMEABLE SEDIMENTS

The majority of sand and gravel that dominate sediments on the inner shelf was deposited by rivers and terrestrial runoff during the last ice age, when the sea level was $\sim 120 \text{ m}$ lower, or was

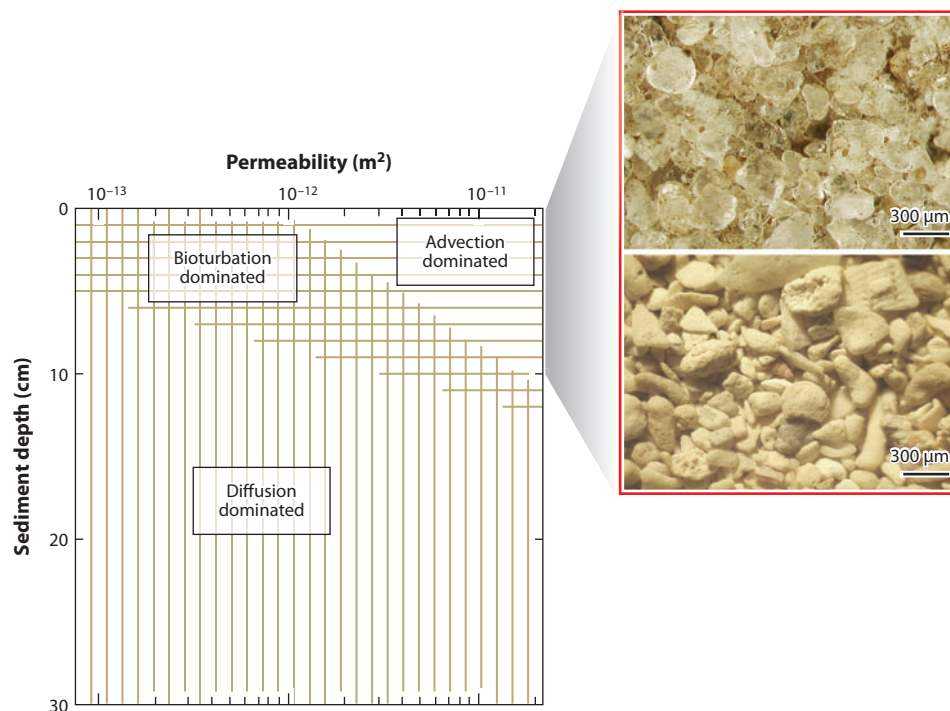


Figure 2

The ranges of dominant transport mechanisms in marine sediments and the two main forms of permeable shelf sediments: silicate sands (*upper inset*) and carbonate sands (*lower inset*). Adapted from Huettel et al. (2003).

produced by calcifying organisms (Emery 1968, Hall 2002, Hayes 1967) (**Figure 2**). The grain size spectrum and sorting of these permeable deposits reflect the effects of cross-shelf transport processes and latitudinal location. The fraction of gravel increases in subpolar and polar regions, whereas finer deposits are more widespread in humid tropical areas, where carbonate sediments are common and high rainfall enhances suspended matter delivery to the coastal zone (McCave 2003, Nittrouer 1981).

Highly permeable sediments can persist only where deposition of fine particles is low or where hydrodynamic or biological processes regularly remove these particles from the bed. Such winnowing results from sediment resuspension, after which fine particles that remain suspended for longer periods are exported by currents to deeper and calmer areas, while sand grains rapidly settle. Repeated cycles of resuspension increase sorting and thereby the permeability of the bed. Hydrodynamic winnowing affects mostly the inner region of the shelf, where the current-induced critical shear velocity (u_*) frequently exceeds the erosion threshold of the sand beds ($u_* \approx 0.7 \text{ cm s}^{-1}$, produced by a flow of approximately 20 cm s^{-1} at 15 cm above the bed) (Wiberg & Smith 1987). A global survey placed the seaward boundary of this zone, the sand-mud transition, at depths of approximately 15, 25, and 50 m for low-, middle-, and high-energy shelf environments, respectively (George & Hill 2008). A second region of coarse sediments is commonly found at the shelf edge, where penetration of surficial geostrophic currents onto the shelf causes strong bottom currents and extensive fields of sand waves (Viana et al. 1998).

Table 1 Drivers of pore-water exchange in permeable shelves and associated conservative flushing rates for the global shelf, calculated per meter of shoreline (from Santos et al. 2012b)

Driver	Flushing rate ($\text{m}^3 \text{m}^{-1} \text{d}^{-1}$)
Tidal pumping (including pumping through barriers)	4
Wave setup at beach faces	6
Groundwater seepage	10
Density-driven exchange (convection)	10
Shear (Brinkman layer)	100
Bioirrigation (pumping by sedimentary animals)	300
Ripple migration	340
Wave pumping	380
Flow-topography interaction	1,000
Total	2,150

As a consequence of the relatively high permeability of the shelf sands, even small pressure asymmetries generated at the surface or within the permeable shelf sands drive pore-water flows through the interstitial space. The flow rate of water through the sand is proportional to the pressure gradient and the permeability of the sand as expressed by Darcy's law (Darcy 1856). In situ permeability measurements in sandy shelf sediments of the northeastern Gulf of Mexico showed permeabilities ranging from 0.3×10^{-11} to $6.1 \times 10^{-11} \text{ m}^2$. The permeability is highest in the upper 10–20 cm of the sediment and then decreases by 50% or more at sediment depths of 40–50 cm (Bennett et al. 2002). This range of permeabilities is typical for sandy shelf sediments, as supported by studies from the North Sea (Janssen et al. 2005b, Reimers et al. 2004, Riedl et al. 1972), Mediterranean Sea (Webb & Theodor 1968), Atlantic Ocean (Jahnke et al. 2000, Reimers et al. 2004), and Pacific Ocean (Sansone et al. 2008).

3. DRIVERS OF PORE-WATER EXCHANGE

The main causes for the pressure gradients that drive water through the surface layers of permeable shelf sands are bottom currents, waves, and pumping activities of sedimentary animals (Table 1). Boundary flows, coupled through viscosity to the pore water of a flat permeable sand bed, generate horizontal pore-water flow in a thin surface layer with a thickness on the order of the grain diameter (Goharzadeh et al. 2005). Despite limited depth penetration, pore-water transport in this Brinkman layer influences the cycling of matter, as it continuously flushes the sediment layer that typically contains the most reactive organic material. Tidal water-level oscillations pump water through sandy beaches and modulate release of coastal aquifers (Charette et al. 2005, McLachlan et al. 1985), and in tropical coasts, tidal pressure gradients pump water through the permeable reef framework and lagoon sands of coral reefs (Tribble et al. 1992). Surface gravity waves rapidly move a pattern of higher (under the wave crest) and lower (under the trough) pressure over the seafloor, resulting in lateral pressure gradients that lead to oscillating pore-water movement and increased exchange at the surface. Waves also effectively enhance pore-water exchange through their orbital water motion, which reaches the seabed where water depth decreases to less than half the wavelength. When the resulting oscillating boundary currents are deflected by protruding or recessed structures on the sediment surface, pressure gradients evolve that drive water into the sand and draw pore water to the surface (Precht & Huettel 2004,

Thibodeaux & Boyle 1987). The migration of sand ripples produced by bottom currents leads to the trapping and release of pore water. Each ripple of a sandy shelf bed acts as a filter system, with currents forcing water into the ripple troughs and slopes and drawing pore water to the surface under the ripple crest (Huettel et al. 1996). Using dye injections into ripples of a sublittoral Mediterranean sand bed, Webb & Theodor (1968) found that fluid is rapidly drawn from sediment depths of 7.5 cm to the surface, implying that substantial volumes of water are filtered through the sand. In situ measurements of pore-water flows using injection of an iodide tracer into Atlantic Bight shelf sands at a water depth of 13 m revealed interfacial flow velocities of up to 50 cm h⁻¹, implying pore-water exchange rates of up to 1,300 L m⁻² d⁻¹ (Reimers et al. 2004).

Benthic animals pump water through permeable shelf sands at rates that rival those of physical mechanisms. Common bottom dwellers of permeable coastal sands include bristle worms of the genus *Arenicola*, which force water through their blind-ending J-shaped burrows into the sediment, thereby moving pore water from ~30-cm sediment depths to the surface at rates of 50–240 L m⁻² d⁻¹ (Riisgård & Banta 1998, Volkenborn et al. 2010). The connection to ground-water aquifers generates deep pore-water circulation in shelf sands that can link biogeochemical processes across sediment layers, with groundwater seepage providing a source of nutrients, metals, carbon, and chemical tracers (Burnett et al. 2003, Charette & Buesseler 2004). Rapid changes in temperature, salinity, and the groundwater tracer ²²⁶Ra in monitoring wells installed 20 km offshore in sandy South Atlantic Bight sediments indicated that pore-water exchange reaches down to sediment depths of several meters (Moore 1999). Salinity and temperature gradients drive convection cells that can extend through the upper centimeters to meters of permeable sediment (Rocha 2000, Webster et al. 1996). On a larger scale, thermal gradients between the warmer shelf environment, heated by the normal geothermal heat flux across the Earth's crust, and the colder ocean can set up geothermal convection in the sloping seafloor that can reach laterally tens of kilometers into the continental shelf (Wilson 2005).

A comprehensive listing of pore-water exchange processes in permeable beds is beyond the scope of this review. In addition to the above-mentioned drivers, other processes such as gas ebullition and sediment compaction cause pore-water flows in coastal sands; interested readers are referred to reviews by Santos et al. (2012b) and Burnett et al. (2003).

4. BIOGEOCHEMICAL SETTINGS IN PERMEABLE SEDIMENTS

The rapid pore-water exchange in permeable seabeds intricately ties the biogeochemical processes in the surface layers to the bottom water and sets the biogeochemical environment in sandy seabeds apart from those in diffusion-dominated fine-grained deposits. Whereas solute transport by molecular diffusion is limited mainly by the temperature-dependent rate of Brownian molecular motion, the rate of advective pore-water flows is a function of the pressure gradients and sediment permeability, and thus can vary over a wide spectrum of velocities and temporal scales. Passing waves impose pressure fluctuations that change over seconds, whereas the hydraulic head driving groundwater seepage may occur at the pace of regional changes in climate. In the surface layer of sandy shelf beds, pore-water flows of 40–50 cm h⁻¹ were recorded with velocity changes at timescales of minutes (Precht & Huettel 2004, Reimers et al. 2004). Even under calm conditions, solute transport from 10-cm depth to the sediment surface may take less than 16 hours, compared with the ~1 month that transport by molecular diffusion would require (Huettel et al. 1996).

Molecular diffusion in muddy sediments works toward an equilibration of concentration gradients; in contrast, complex multidimensional pore-water flows in sands produce concentration gradients. Ubiquitous diffusion and counterdiffusion cause bidirectional exchange throughout the sediment surface, whereas advective interfacial water exchange separates areas of transport into

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and out of the sediment, creating zones with distinctly different biogeochemical characteristics (Huettel et al. 1998). Areas of in- and outflow can be distributed as regularly as the ripple fields they are associated with (Packman & Brooks 2001) or as randomly as the bottom topography produced by bottom dwellers (Volkenborn et al. 2007, Ziebis et al. 1996a).

By increasing the surface area of active sites where biogeochemical reactions occur and extending the reaction zones to greater depths, the spatial patterns of the pore-water flows result in enhanced sediment metabolism, similar to the effect of animal burrows in muddy sediments. Fast-moving pressure fields, such as those associated with waves, cause changes in pore-water flow direction that enhance mixing through rotational dispersion (Webster & Taylor 1992). Slower-moving pressure fields, such as those associated with migrating ripples, generate pore-water flow fields that scale with the horizontal length scale of the relief, causing the pressure perturbation; for ripples on well-sorted sand beds, the pore-water flow fields thus may reach as deep as half the distance between neighboring ripple crests (Huettel & Webster 2000). Lateral ripple movement shifts the up- and downwelling zones of this pore-water flow field, thereby generating redox oscillations that enhance organic matter degradation (Aller 1994) and cause sorption and desorption processes at the sediment grain surfaces (Keil & Hedges 1993).

As these processes often work on timescales different from those of the changes in the pore-water flow pattern, hysteresis effects may result (Middelburg & Levin 2009). Intrusion of water up- and downstream from sand ripples creates oxygen gradients that match the highest oxygen supply in the uppermost sediment layer with the highest concentrations of fresh organic carbon, thereby maximizing aerobic decomposition (Huettel & Rusch 2000). Rapid transport of oxygen into deeper sediment layers produces subsurface zones of manganese and iron oxidation and hot spots of nitrification (Huettel et al. 1998). Anoxic pore-water flows, drawn to the surface at ripple crests, can act as conduits for reduced substances from deeper sediment layers to the water column. During periods of slow boundary currents and stationary ripples, this process leads to the release of dissolved organic carbon, ammonium, and ferrous iron from sandy seabeds, a process that is blocked during phases with stronger currents (**Figure 3**). Such currents flush the ripple crests and upper sediment layer, producing a continuous oxidized surface layer that acts as an effective barrier for reduced substance release from the bed. The strength of the boundary-layer flows therefore determines not only the magnitude of solutes released from the sand bed but also the quality of these solutes.

5. PARTICLE FILTRATION

In contrast to the muddy seafloor, where sedimenting particulate matter accumulates at the surface, the relatively large pores of sandy seabeds allow the settling of particles into the upper layer of the bed and the filtration of suspended colloidal material deeper into the subsurface layer with interfacial water flows. Within hours, energy-rich organic particles can be carried to sediment depths of several centimeters, thereby influencing the sedimentary food web and biogeochemical activity (Huettel & Rusch 2000). Most organic particles may settle to the seafloor as aggregates, with a size range comparable to or larger than that of the sediment grains (e.g., marine snow), and then form a fluff layer on the sediment surface (Stolzenbach et al. 1992). Shear forces associated with boundary-layer currents cause disaggregation of this flocculent material, producing smaller particles (Jago et al. 2002). When these particles are $\sim 1/20$ th of the sediment grain size (e.g., 10- μm phytoplankton cells in 300- μm sand), they are readily transported with the pore-water flow into the sediment (McDowell-Boyer et al. 1986). Here, flow through the sediment pore spaces separates mixtures of particles according to their size, shape, and surface charge and the pore-space geometry (Huettel et al. 1996), producing layers of particles with similar transport



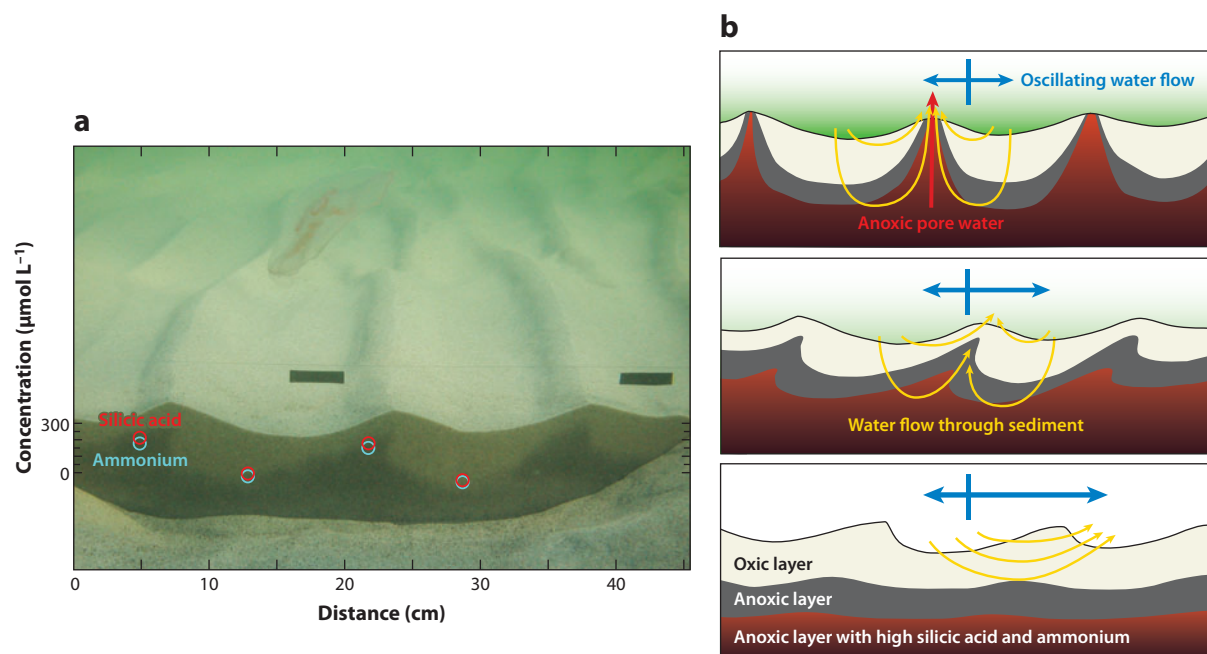


Figure 3

(a) Cross section of permeable sand sediment, showing dark zones stained by upwelling anoxic pore water rich in black iron sulfides. The anoxic pore water is enriched in silicic acid and ammonium (circles). (b) Changes in the wave-induced pore-water flow pattern with increasing unidirectional bottom currents. The blue horizontal arrows represent the oscillating water flow, with the vertical line denoting the center of the flow orbital; the yellow arrows represent water flows through the sediment; and the red vertical arrow represents the pathway of deep, anoxic pore water through the sediment into the overlying water. (Top) Oscillating bottom currents caused by waves pump pore fluid to the surface, and anoxic water with high nutrient concentrations is released to the overlying water. (Middle) When unidirectional currents are superimposed on the oscillating bottom currents caused by waves, lateral ripple migration increases and the zones of anoxic pore water upwelling are tilted and start disconnecting from the sediment surface. (Bottom) When unidirectional currents become stronger, lateral pore-water flows dominate in the surface layer, and the anoxic pore fluid no longer reaches the sediment surface. Reduced substances like ammonium and ferrous iron are then oxidized in the flushed layer before they can reach the sediment surface. Vertical and horizontal fluctuations of the oxic-anoxic boundary caused by ripple migration and bottom currents can thereby promote coupled nitrification-denitrification. In the middle and bottom graphs, a unidirectional flow (from left to right) is superimposed on the oscillating water flow, and therefore the flow oscillation becomes asymmetrical and the flow to the right is stronger than the flow to the left. Adapted from Precht et al. (2004).

characteristics that can influence and create biogeochemical reaction zones. Particles in the size range of microorganisms can travel tens to hundreds of centimeters through permeable sand (Harvey et al. 1995); however, isotope and chlorophyll profiles measured in shelf sands suggest that most of the short-term vertical particle transport is restricted to the upper 10–20 cm of the bed (Bacon et al. 1994).

The resulting particle distribution in permeable beds is not even but rather reflects the locations of the water in- and outflow areas. The slopes of protruding and recessed sediment topography typically show the deepest particle penetration and highest accumulation rates (Pilditch & Miller 2006). Upwelling pore water under protruding sediment relief or that caused by groundwater seeps impedes particle penetration into the sand.

Together, these processes result in a complex but organized distribution of fine particulate matter in permeable seabeds. Sedimentary particle filtration is a self-limiting process, as the permeability of the sand bed decreases rapidly when the fraction of fine particles exceeds ~10% of

the sediment volume (Aringhieri 2006). Particles filtered into the sand cannot be easily dislodged even if the flow rate increases, but flow reversal in the interstitial space can remobilize them and thereby also allow export from the sediment (Huettel et al. 2007). This removal process is not very effective, and without frequent winnowing, the sand bed eventually becomes clogged.

6. THE ROLE OF FAUNA

Bioturbation and bioirrigation activities of benthic fauna affect sediment permeability, particle transport, and pore-water exchange and thereby profoundly affect benthic-pelagic coupling and the biogeochemical processes in the bed (Aller 1978, Rhoads et al. 1977). Owing to frequent resuspension, compaction of the sand surface layer is so low that fish like sand eels (*Ammodytes tobianus*) and flounders (e.g., *Platichthys flesus* and *Pseudopleuronectes americanus*) can easily bury themselves in it and breathe while hiding. At realistic winter densities of 60 m^{-2} , buried sand eels enhance the oxygen uptake of the sand bed by a factor of up to two, with half of the flux caused by their respiration (Behrens et al. 2007). Mud shrimp (*Callinassa truncata*) enhance sediment oxygenation around their 50–80-cm-deep burrows in Mediterranean sands; at abundances of up to 120 m^{-2} , they eject $2\text{--}3 \text{ kg m}^{-2} \text{ d}^{-1}$ of fine sand from their burrow openings, which, through lateral export of this material, maintains the coarse grain size of the bed (Ziebis et al. 1996a).

Similarly, the polychaete *Arenicola marina* maintains high sediment permeability through selective ingestion of fine particulate matter at its feeding depth and defecation at the surface (Volkenborn et al. 2007). Through bioirrigation, *A. marina* stimulates sediment oxygen uptake and CO_2 release of up to 80% while inhibiting anaerobic decomposition, as indicated by the 66% lower sulfate reduction rates in areas where *A. marina* is present (Banta et al. 1999). Nitrification is stimulated where *A. marina* pumps oxygen-rich water into the sediment, whereas concentrations of silicic acid and ammonium are reduced in the sand above *A. marina* feeding depths (Huettel 1990). Structures as small as $700 \text{ }\mu\text{m}$ exposed to water flows as low as 3 cm s^{-1} produce advective pore-water exchange in permeable sand beds. Thus, tracks produced on the sediment surface by foraging animals, mounds of *A. marina* fecal matter, protruding siphons of clams, and shell fragments scattered on the sediment surface all lead to pore-water exchange, and realistic abundances of such structures enhance interfacial solute flux in coastal sands by factors of up to 10 (Huettel & Gust 1992).

In shelf sands, the relatively large pores flushed with oxygen-rich water harbor a highly diverse interstitial meiofauna community that stimulates carbon turnover through grazing activities and by enhancing bacterial productivity (Giere 1993). A pulse-chase experiment showed that ^{13}C -labeled sedimentary microalgae are rapidly displaced from the surface of an intertidal sand bed down to a sediment depth of 6 cm through ingestion by bottom dwellers; nematodes became enriched after only 1 hour, and bacteria showed maximum labeling after 1 day (Middelburg et al. 2000), revealing the efficiency of carbon transfer in the interstitial food web. Meiofauna can penetrate 50–60 cm deep into the sand bed, and through their vertical migration maintain open pore space and sediment permeability (Malan & McLachlan 1985). Many phototrophic microorganisms (e.g., cyanobacteria and dinoflagellates) perform periodic vertical migrations in sand beds for distances exceeding 10 cm, which allows them to avoid resuspension and grazing and to access higher nutrient concentrations in deeper sediment layers (Kingston 2002). Through this migration, microorganisms can function as organic matter and nutrient pumps within sandy sediments. Likewise, planktonic microalgae can be transported with pore-water flows through the surface layer of rippled sand beds and can be released again to the water column, which may be a mechanism for phytoplankton to access the higher nutrient concentrations in the sediment (Huettel et al. 2007).



7. BENTHIC PRIMARY PRODUCTION

On the inner shelf, the shallow water depth allows light to reach the seafloor, thereby facilitating benthic photosynthesis. Minimum average light intensities at which benthic microalgal production has been measured across arctic to tropical climates range from 0.04 to 1.2 mol photons $\text{m}^{-2} \text{d}^{-1}$ (Cahoon et al. 1999), and more than 100 obligate benthic diatom species were found in North Carolina continental margin sediments collected at depths of 67–191 m (McGee et al. 2008). Based on a conservative light flux of 0.4 mol photons $\text{m}^{-2} \text{d}^{-1}$ as the minimum daily compensation irradiance, approximately one-third ($8.6 \times 10^6 \text{ km}^2$) of the shelf bottom receives sufficient light for benthic microalgal production (Gattuso et al. 2006). This area is similar to that of the inner shelf, with water depths of less than 30 m and a seafloor dominated by permeable sands. The abundance of microphytobenthos in permeable sediments varies from approximately 10^5 to 10^7 cells cm^{-3} , with maximum biomass observed in spring or summer in the upper 5 cm of sediment and chlorophyll values typically ranging from 10 to 50 mg m^{-2} (Cahoon et al. 1999, Macintyre et al. 1996). When nutrients become limited during summer, up to 70% of the carbon fixed by the microphytobenthos may be excreted as carbohydrates (extracellular polymeric substances) that serve as an important carbon source for the benthic bacteria (Underwood & Kromkamp 1999). Owing to the high mixing intensity of the sediment surface layer, the majority of the diatoms live attached to sand grains and may be distributed to depths of 20 cm or more (Meadows & Anderson 1966). Light can penetrate 1–5 mm into sand beds (Kühl & Jørgensen 1994); thus, microalgae buried deeper than 5 mm cannot photosynthesize, and some are capable of heterotrophic metabolism under dark conditions (Hellebust & Lewin 1977).

Primary production of the benthic phototrophs is a major source of organic matter in permeable coastal sands and is within a factor of two of primary production in the overlying waters. In Onslow Bay on the sandy North Carolina continental shelf (water depths of 15–41 m), gross benthic microalgal production averages 21 $\text{mmol C m}^{-2} \text{d}^{-1}$, compared with an average integrated water column production of 23 $\text{mmol C m}^{-2} \text{d}^{-1}$ (Cahoon & Cooke 1992). Three degrees farther south, on the South Atlantic Bight shelf, Jahnke et al. (2000) and Nelson et al. (1999) measured gross benthic primary production rates that averaged $33 \pm 22 \text{ mmol C m}^{-2} \text{d}^{-1}$ (water depths of 14–40 m, May–September 1996), compared with water column productivity that reached $57 \pm 15 \text{ mmol C m}^{-2} \text{d}^{-1}$. Benthic chamber measurements conducted during a calm summer period at this site showed benthic gross primary production decreasing from 69 $\text{mmol C m}^{-2} \text{d}^{-1}$ at 14-m depth to 13 $\text{mmol C m}^{-2} \text{d}^{-1}$ at 40-m depth (Jahnke et al. 2000). The annual averages, however, are much lower; based on long-term time series of benthic light measurements, Jahnke et al. (2008) calculated annual benthic production for South Atlantic Bight sands at 27-m depth ranging from 0.9 to 5.3 $\text{mol C m}^{-2} \text{y}^{-1}$. Assuming similar rates in colder and warmer climate zones, the annual gross benthic microphytobenthos production in the global inner shelf (water depth of <25 m, $7.4 \times 10^6 \text{ km}^2$) would range between 7 and 39 Tmol C y^{-1} . For the total global shelf, Duarte et al. (2005) estimated an average production of 135 Tmol C y^{-1} , more than three times higher.

Approximately $1.5 \times 10^6 \text{ km}^2$ of the global inner-shelf bottom has the minimum temperature of 16°C and receives the minimum light intensities of 1.4 mol photons $\text{m}^{-2} \text{d}^{-1}$ that hermatypic corals need for growth (Gattuso et al. 2006). The global gross primary production of these corals' symbiotic microalgae (zooxanthellae, mostly dinoflagellates) is estimated to reach 86 Tmol C y^{-1} (Duarte et al. 2005). Together with the carbonates formed by benthic foraminifera, calcifying algae, sponges, and benthic invertebrates (e.g., sea urchins and molluscs), the debris of coral skeletal material produces the biogenic sands that cover the tropical inner shelves (Ball 1967). In addition to these microalgae, macroalgae and seagrasses contribute to the benthic primary production of the



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sand shelf. Although macroalgae are best known to colonize hard substrates of rocky shorelines, these phototrophs grow abundantly in the sandy inner shelf, especially in the tropics (Cebrián & Duarte 1994). Their minimum light requirements ($0.44\text{--}1.6\text{ mol photons m}^{-2}\text{ d}^{-1}$; Gattuso et al. 2006) and depth range are similar to those of benthic microalgae. In subtropical and tropical environments, species of the green calcifying macroalgae *Halimeda* and *Penicillus* supply up to 61% of the carbonate sands (Hudson 1984). Macroalgae globally cover approximately $1.4 \times 10^6\text{ km}^2$ of the shelf, with a gross primary production of 432 Tmol C y^{-1} (net ecosystem production of 185 Tmol C y^{-1}), which thus may exceed that of the shelf microphytobenthos by a factor of three (Duarte et al. 2005).

With a minimum light requirement of $3\text{--}5\text{ mol photons m}^{-2}\text{ d}^{-1}$ (Duarte 1991), seagrasses typically do not colonize sediments at water depths greater than 30 m (median depth of 4.4 m; Duarte 1991), and they may cover approximately 8% ($0.6 \times 10^6\text{ km}^2$) of the inner shelf (area with water depths of $<25\text{ m}$) (Duarte & Chiscano 1999). Globally, seagrass gross primary production is estimated to reach 52 Tmol C y^{-1} (Duarte et al. 2005); net carbon production reaches 13 Tmol C y^{-1} , suggesting that seagrasses may be responsible for 15% of the total excess carbon produced in the global ocean (Duarte & Cebrián 1996). Owing to their production of belowground biomass and fiber-rich detritus and their particle-trapping efficiency, seagrasses can turn sandy sediments into organic-rich sandy muds, and seagrass meadows are estimated to bury 2.3 Tmol C y^{-1} , or roughly 10% of the estimated yearly organic carbon burial in the oceans (Duarte & Chiscano 1999, Fourqurean et al. 2012). The colonization by seagrasses can thus change nonaccumulating permeable shelf sands with rapid aerobic degradation of organic matter into accumulating muddy anaerobic sediments that are sites of substantial carbon burial (Fourqurean et al. 2012). Based on the total production of microphytobenthos, zooxanthellae, macroalgae, and seagrasses, the integrated global gross benthic primary production on sandy shelves may reach 705 Tmol C y^{-1} , with a net production of 195 Tmol C y^{-1} (Duarte et al. 2005).

8. THE MICROBIAL COMMUNITY OF PERMEABLE SEDIMENTS

The abundance, community composition, and distribution of microorganisms remain understudied in permeable sediments compared with those of their counterparts in muddy deposits. Early work observed an inverse correlation between microbial abundance and surface sediment grain size (Deflaun & Mayer 1983), implying that sands harbor relatively low microbial numbers, as the sand-specific surface area is two to three orders of magnitude lower than that of fine-grained sediments. The population density of bacteria on sediment grains was found to be confined to a relatively narrow range of 1 cell per $70\text{--}300\text{ }\mu\text{m}^2$, or approximately 1–3% of the particle surface area (Fenchel 1970). However, more recent studies based on improved extraction methods have shown that total cell numbers in coastal sands reach $10^9\text{ cells cm}^{-3}$ (e.g., Böer et al. 2009, Rusch et al. 2003), which is approximately 1,000 times more abundant than those in the same volume of typical seawater. These microbial abundance estimates overlap with observations from muddy sediments.

Although the bacterial contribution to the sand's carbon pool usually does not exceed 10%, or $10\text{--}100\text{ }\mu\text{mol C cm}^{-3}$ (Köster & Meyer-Reil 2001, Rusch et al. 2003), the heterotrophic bacterial community can be highly active, with a seasonally changing gross secondary productivity of $30\text{--}180\text{ mmol C m}^{-2}\text{ d}^{-1}$ and a biomass turnover time of 2–18 days in carbon-poor sands (Böer et al. 2009). More than 99% of the bacteria in sand may live attached to the grain surfaces (Rusch et al. 2001), where they benefit from close association with organic substrate adsorbed to the mineral surfaces (Keil & Hedges 1993) and the pore-water flows that provide electron acceptors and remove metabolites. Contact with solid surfaces triggers exopolymer synthesis in bacteria to



secure the cells and their progeny in the favorable environment, and this mucus production can reduce sediment permeability (Vandevivere & Baveye 1992).

Microbes grow mostly in cracks and depressions on sand grains, which may protect them from grazing and from abrasion when sands move (Miller 1989). The microtopography of the sediment grains thus strongly influences bacterial colonization (Meadows & Anderson 1966, 1968), and the numerous pores and rugged surfaces of biogenic carbonate sands compared with crystalline mineral sands lead to relatively higher microbial abundances in subtropical and tropical reef sands (Wild et al. 2006). The different mineralogy of these sands may also contribute to significant differences in the microbial community structure (Schöttner et al. 2011). As pore water flows and as physical and chemical interfaces in permeable sediments change frequently, benthic microbes experience highly variable biogeochemical conditions, and thus they may have evolved more versatile metabolisms (Canfield & Des Marais 1991, Gao et al. 2010). RNA-based clone libraries and stable isotope probing experiments have suggested that sand microbial communities are poised to respond rapidly to short-term periodic pulses of growth substrates (Mills et al. 2008).

Although microorganisms have been shown to be abundant and diverse in marine sands, less information is available on the distribution and function of specific microbial groups. Relatively few studies have employed the latest next-generation gene sequencing approaches, and previous cultivation-independent studies are lacking in sequencing depth and phylogenetic resolution. Studies to date have indicated that permeable sediments contain diverse bacterial communities that are dominated by members of the Gammaproteobacteria and Alphaproteobacteria classes (Böer et al. 2009, Hunter et al. 2006, Kostka et al. 2011). In addition, members of the following microbial groups are routinely observed in sequence libraries at the phylum/class taxonomic level: Deltaproteobacteria, Actinobacteria, Cyanobacteria, Acidobacteria, Bacteroidetes/Chlorobi, Chloroflexi, and Firmicutes. Studies have also indicated that enhanced transport and mixing in the permeable bed results in a relatively even distribution of microbial taxa throughout the upper 5–10 cm of sediment (Mills et al. 2008).

Although few comparisons are available, bacterial communities in sands are generally more diverse than bacterioplankton but not as diverse as the bacterial communities of marine muds or soils (Kostka et al. 2011). A time series assessing bacterial community composition in intertidal North Sea sands via pyrosequencing of ribosomal genes revealed that only 3–5% of all bacterial types of a given sediment depth zone were present at all times, whereas 60–70% of the bacterial types occurred only once in the six samples recovered at 2–3-month intervals (Gobet et al. 2012). These findings imply that a small proportion of continuously abundant resident bacterial types perform the major biogeochemical processes in the sand, whereas a large number of rare types that are replaced at high rates have little effect on the bulk biogeochemical functions. Notably, little to no information is available on microorganisms affiliated with Archaea or microbial eukaryotes in permeable sediments. Cultivation-based studies and studies employing metagenomics or other “-omics” approaches are lacking, and the majority of previous work has targeted small-subunit rRNA genes. Thus, linkages between specific microbial groups and ecosystem function remain difficult to establish in permeable sediments.

Enzyme assays have provided direct evidence for the initial stages of organic matter degradation by microbes in permeable sediments. For optimal use of the intermittent supply of organic matter, the concentrations and activities of extracellular enzymes in the pore space are critical. Hydrolases that decompose carbohydrates are considered rate limiting in the microbial degradation of organic matter, and in a comparison of polysaccharide hydrolysis rates in Baltic muds, sandy muds, and sands, Arnosti (1995) found that the highest rates occurred in subsurface sand samples. Similarly, hydrolytic activities of extracellular exoenzymes in North Sea intertidal sands can be as high as those in muddy, organic-rich sediments (Böer et al. 2009), with rates that would allow a complete

hydrolysis of the subsurface ethylenediaminetetraacetic acid (EDTA)-extractable carbohydrate pool (sediment depths of 10–15 cm) within 5 days. In the upper 5 cm of Middle Atlantic Bight sand, β -glucosidase activities reach $12 \text{ nmol cm}^{-3} \text{ h}^{-1}$, and aminopeptidase rates reach $70 \text{ nmol cm}^{-3} \text{ h}^{-1}$ (Rusch et al. 2003). Such high aminopeptidase rates may be common in organic-poor sands, where microbes rely on peptidases to obtain sufficient amounts of organic nitrogen (Mudryk & Podgorska 2005). Through the relatively high rates of fluid exchange between permeable sediment and the overlying water, the exoenzymes released by sedimentary bacteria to the pore water can also affect water column decomposition processes by enhancing the spectrum of enzymes and facilitating hydrolysis of high-molecular-weight organic matter in the boundary layer (Arnosti et al. 2009).

9. RESPIRATION AND CARBON TURNOVER

On the shallow shelf, high productivity and the availability of oxygen fuels high levels of decomposition activity, and respiration rates and nitrogen regeneration in the sediments can reach more than 80% of the total system activity (Middelburg & Soetaert 2004). Decomposition activity is reflected in sedimentary oxygen uptake, which peaks in the nearshore environment. Although this oxygen consumption cannot be directly equated with organic matter decomposition because it ignores electron sinks like N_2 release from denitrification and pyrite burial (Glud 2008), the rates can provide an estimate of total respiration with the assumption that the reoxidation of anaerobic respiration products occurs mainly within the sediment (Canfield et al. 1993). The extent of reoxidation processes is reflected by the balance of oxygen consumption and dissolved inorganic carbon production, as the latter is the final product of all respiration pathways. The complete oxidation of Redfield organic matter produces respiration coefficients of 1.3 (Hedges et al. 2002). In South Atlantic Bight sands, a thick, light-colored sand layer and respiration coefficients close to 1 indicate that the oxidation of anaerobic respiration products and reduced inorganic substances in these highly permeable sands is of minor importance and is completed within the seabed (Jahnke et al. 2000, 2005). Similar results have been reported for the North Sea (Billerbeck et al. 2007, Kristensen et al. 1997) and Baltic Sea (Cook et al. 2007).

The complete inhibition of oxygen uptake in shelf sands after treatment with formalin supports the idea that the oxygen consumption is mainly biological and that chemical oxidation processes are of minor importance (Hargrave 1972). Measurements in Mid-Atlantic Bight sands suggested that fresh organic matter that had filtered into the sands and benthic primary production are the main drivers for benthic metabolism, with sediment oxygen consumption correlated with sediment chlorophyll *a* content and not with sediment organic carbon content or temperature (Laursen & Seitzinger 2002). In an in situ pulse-chase experiment using labeled phytoplankton settling on sandy sediment in the southern North Sea, 62% of the recovered label was found in bacteria after only 12 hours, and 6 days into the experiment, most of the material was mineralized to CO_2 (Bühning et al. 2006), indicating rapid turnover of the fresh organic material. The organic content of sands is typically less than 0.1% of the sediment dry weight (Burdige 2006), and after normalizing to surface area, we find that sediment particles consume $1\text{--}100 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Hargrave 1972). Therefore, sand oxygen uptake under stagnant, diffusion-dominated conditions is a fraction of that observed in finer-grained muds.

Owing to low organic content and relatively rapid pore-water transport, only a fraction of the oxygen circulated through the surface layer of permeable sand beds may be consumed. For example, in shallow Baltic and North Sea sands, only $\sim 30\text{--}70\%$ of the oxygen supplied to the sediment is used (Cook et al. 2007). Nevertheless, flux measurements with instruments that include or mimic advective pore-water exchange revealed benthic oxygen consumption rates in sands that compete in magnitude with those reported for organic-rich fine-grained deposits (Table 2). Comparison



Table 2 Measured rates of gross primary production (GPP), respiration (R), net ecosystem metabolism (NEM), and denitrification for silicate and carbonate shelf sands

Location	Depth range (m)	Sand type ^a	Permeability ($\times 10^{-11} \text{ m}^2$)	Production and respiration ($\text{mmol C m}^{-2} \text{ d}^{-1}$)			Denitrification ($\text{mmol N m}^{-2} \text{ d}^{-1}$)	Method ^b	Reference(s)
				GPP	R	NEM			
Northeast Gulf of Mexico	0–10	S	1.3	—	283	—	—	E	Berg & Huettel 2008
	0–10	S	4.6	—	6–8	—	0.1–1.9	C	Gihring et al. 2010
	0–10	S	1.3	16	75	–59	—	C	Berg & Huettel 2008
West Falmouth Harbor, Massachusetts	0–10	S	1.8	11	19	–7	—	E	Berg et al. 2013
	0–10	S	1.8	25	17	8	—	E	
Mid-Atlantic coast, Virginia	0–10	S	2.5	–8	10	–18	—	E	Hume et al. 2011
	0–10	S	2.5	19	46	–27	—	E	
	0–10	S	2.5	42	104	–62	—	E	
South Atlantic Bight, Georgia	10–20	S	4.7	60	56	4	—	C	Jahnke et al. 2000
	20–30	S	4.7	31	32	–1	—	C	
	30–40	S	4.7	15	24	–9	—	C	
Onslow Bay, North Carolina	10–20	S	—	37	35	12	—	C	Cahoon & Cooke 1992
	20–30	S	—	59	37	48	—	C	
	30–40	S	—	16	40	25	—	C	
Mid-Atlantic Bight	10–20	S	2.2	0	14	–14	1.4	C	Laursen & Seitzinger 2002
	10–20	S	2.2	1	11	–10	1.7	C	
North Sea	0–10	S	2	32	51	–18	—	C	Cook et al. 2007
	10–20	S	0.3	—	22	—	—	C	Janssen et al. 2005b
	10–20	S	2.6	—	28	—	—	C	
	10–20	S	7.5	—	21	—	—	C	
North Sea intertidal zone	0–10	S	4	6	32	–26	—	C	Billerbeck et al. 2007
	0–10	S	3.9	22	27	–5	—	C	
Baltic Sea	0–10	S	2.9	23	46	–24	—	C	Cook et al. 2007

(Continued)

Table 2 (Continued)

Location	Depth range (m)	Sand type ^a	Permeability ($\times 10^{-11} \text{ m}^2$)	Production and respiration ($\text{mmol C m}^{-2} \text{ d}^{-1}$)			Denitrification ($\text{mmol N m}^{-2} \text{ d}^{-1}$)	Method ^b	Reference(s)
				GPP	R	NEM			
Heron Island, Australia	0–10	C	10	130	241	–110	—	C	Santos et al. 2011
	0–10	C	6	87–99	77–87	10–12	0.4–5.9	C	Eyre et al. 2008, Glud et al. 2008
	0–10	C	12	—	54	—	—	C	Wild et al. 2004a
	0–10	C	12	—	49	—	—	C	
	0–10	C	12	—	65	—	—	C	
	0–10	C	12	—	55	—	—	C	
	0–10	C	12	—	65	—	—	C	Wild et al. 2004b
	0–10	C	12	—	72	—	—	C	
Southwest lagoon of New Caledonia	10–20	C	—	—	33	—	—	C	Boucher et al. 1994
	10–20	C	—	—	26	—	—	C	Grenz et al. 2003
	10–20	C	—	—	42	—	—	C	

^aS, silicate; C, carbonate.^bE, eddy correlation; C, chamber.

of oxygen fluxes recorded in benthic advection chambers under diffusion-dominated (little or no flow) and advection-dominated settings suggests that current-induced pore-water exchange can enhance the oxygen uptake in permeable shelf sands by two- to threefold (Janssen et al. 2005b). This magnitude of respiration enhancement was confirmed for silicate sands in temperate Baltic and North Sea sands (Cook et al. 2007) as well as for tropical carbonate sands (Glud et al. 2008, Rasheed et al. 2004). These findings are supported by measurements using the noninvasive eddy correlation technique (Berg et al. 2003) that showed a doubling of oxygen flux in permeable Middle Atlantic Bight sediments following a tripling of current flow velocity ($20 \text{ mmol m}^{-2} \text{ d}^{-1}$ at 5 cm s^{-1} compared with $40 \text{ mmol m}^{-2} \text{ d}^{-1}$ at 15 cm s^{-1}) (Berg et al. 2013). Because the eddy correlation technique measures flux at natural flow conditions, it similarly showed that wave orbital motion can have a strong influence on oxygen consumption rate in permeable coastal sands, with a doubling of the oxygen flux following a tripling of significant wave height ($50 \text{ mmol m}^{-2} \text{ d}^{-1}$ at 6-cm wave height compared with $100 \text{ mmol m}^{-2} \text{ d}^{-1}$ at 18-cm wave height) (Berg & Huettel 2008, Hume et al. 2011). In situ pore-water measurements at the 12-m-deep Kilo Nalu Nearshore Reef Observatory in Hawaii confirmed the effect of waves and suggested a quadrupling of the oxygen content in these carbonate sands following a doubling of the wave-generated boundary flow (Fogaren et al. 2013).

A lasting enhancement of oxygen consumption through increased advective pore-water exchange also requires an enhanced supply of oxidizable substances to the sediment. If this supply ceases, the advective oxygen flux will converge on a diffusive flux that reflects the decay of organic matter present in the oxic zone and the oxidation of reduced substances that diffuse upward from



deeper sediment strata into the flushed sand layer. The high oxygen fluxes observed in permeable shelf sands emphasize the role of fresh organic matter filtration into the bed and benthic primary production. As the quantity and quality of organic matter supply to the sediment is modulated by sunlight, temperature, nutrient availability, and terrestrial inputs (Hartwig 1978), this advective flux enhancement changes on timescales of minutes to seasons. For example, in Middle Atlantic Bight shelf sands, the same pore-water flow rate enhances sedimentary oxygen consumption in May by approximately twice as much as it does in July, reflecting the effects of higher degradability of organic matter in spring (Rusch et al. 2006). Advective oxygen flux enhancement in July corresponded to an increase by $\sim 30 \mu\text{mol m}^{-2} \text{d}^{-1}$ for every $1 \text{ L m}^{-2} \text{d}^{-1}$ flushed through a 4-cm-thick oxic sediment layer (Reimers et al. 2004). At a measured in situ flushing rate reaching $1,300 \text{ L m}^{-2} \text{d}^{-1}$, permeable Middle Atlantic Bight shelf sands at 13-m depth consumed approximately $40 \text{ mmol m}^{-2} \text{d}^{-1}$. Measurements using the eddy correlation technique, which allows fluxes to be measured on short timescales, revealed that in permeable sands, oxygen fluxes calculated for 15-minute intervals can change by a factor of five within 1 hour, underlining the high temporal dynamics of the sedimentary oxygen consumption (Berg et al. 2013).

Although some of these variations may be caused by processes in the benthic boundary layer (Holtappels et al. 2011), the rapid changes in flux reflect the prompt response of aerobic microorganisms colonizing the sand grains to advective organic matter and oxygen supply (Ziebis et al. 1996b). Advective pore-water flows that pump approximately $1,000 \text{ L m}^{-2} \text{d}^{-1}$ of water containing $240 \mu\text{mol O}_2 \text{ L}^{-1}$ through the upper 4 cm of Mid-Atlantic Bight shelf sands can theoretically provide $240 \text{ mmol O}_2 \text{ m}^{-2} \text{d}^{-1}$ to the benthic microbial community. Because bacterial hydrolysis of structurally complex macromolecules as found in plant detritus is much faster under aerobic conditions than under anaerobic conditions (Kristensen et al. 1995), the advective supply of oxygen to the sedimentary microbial community facilitates the effective degradation of organic particles filtered into the surface layers of the shelf sands, resulting in their relatively high oxygen consumption rates. This degradation efficiency may explain why half of the total metabolic carbon turnover in the inner South Atlantic Bight shelf occurs within the sand sediments (Jahnke et al. 2005). Duarte et al. (2005) estimated that the global net ecosystem metabolism for shelf sediments colonized by microphytobenthos is negative ($-31 \text{ Tmol C y}^{-1}$)—i.e., the sediments consume more than they produce. In contrast, carbonate sands, despite their high aerobic decomposition activities, can be a net source of oxygen owing to high benthic photosynthesis rates. These sediments also act as a sink of H^+ , with the strength of this H^+ sink being a function of pore-water flushing rate (Santos et al. 2011). These recent findings suggest that the metabolism of permeable sands can play a major role in proton cycling in tropical environments and constitute a currently unknown feedback to ocean acidification.

10. NITROGEN CYCLING IN PERMEABLE SEDIMENTS

Because the cycling of carbon is coupled to that of nitrogen, the intense production and respiration processes in shelf sands suggest that the coastal environment is a significant sink for land-derived nitrogen (Middelburg & Soetaert 2004). In the aerobic surface layers of the sand, ammonium (NH_4^+) released during the decomposition of sedimentary organic matter is nitrified to nitrite (NO_2^-) and subsequently to nitrate (NO_3^-). Supported by pore-water flushing and intense recycling, this nitrification can account for as much as 71% (average 33%) of oxygen demand in Mid-Atlantic Bight sands (Laursen & Seitzinger 2002). Benthic microalgae act as effective filters for inorganic nitrogen at the sediment surface and can incorporate up to 100% of the nitrogen remineralized in the sediment (Sundbäck et al. 2006), thereby minimizing the loss of dissolved nitrogen from the seabed. This allows sand sediments in low-nitrogen areas to be highly productive through



closed nitrogen recycling (Miyajima et al. 2001, Sundbäck et al. 2000). Cyanobacteria and other microorganisms colonizing the organic-poor shelf sands can fix inorganic nitrogen, although this process may be of minor importance for the nitrogen input and turnover within the sediment (Nixon & Pilson 1983). Nitrogen fixation in tropical carbonate sands (Miyajima et al. 2001) may be an exception and account for a much larger fraction of ammonium turnover than it does in temperate sands (Capone et al. 1992). Nitrite and nitrate produced within the sediment or transported into the bed by pore-water flows provide electron acceptors for denitrifying and anammox (anaerobic ammonium oxidation) bacteria (Hunter et al. 2006); these bacteria reduce dissolved inorganic nitrogen to nitrous oxide (N_2O) and N_2 gas that can escape to the atmosphere, thereby converting the sediments into nitrogen sinks.

Advective pore-water exchange can increase sedimentary denitrification through increased NO_3^- supply from the water column (Rao et al. 2008), and strong flushing can also reduce coupled nitrification-denitrification owing to rapid release of NH_4^+ from the sediment, bypassing nitrification (Cook et al. 2006, Kessler et al. 2012). Nonetheless, nitrification within the sediment may supply more than 85% of the nitrate required for the observed denitrification in North Sea sands (Sundbäck et al. 2000, Van Raaphorst et al. 1992), and this coupled nitrification-denitrification is estimated to support 90–100% of total denitrification in Mid-Atlantic Bight sands (Laursen & Seitzinger 2002). Denitrification in Mid-Atlantic Bight sands removes $1.7 \text{ mmol N m}^{-2} \text{ d}^{-1}$ on average, with the variation proportional to sediment oxygen flux, suggesting that a large fraction of denitrification in continental shelf sands is directly linked to oxygen consumption and degradable organic matter supply to the sediment (Seitzinger & Giblin 1996). The optimum of coupled nitrification-denitrification efficiency may be reached at sediment carbon loadings of $4\text{--}8 \text{ mol C m}^{-2} \text{ y}^{-1}$ (Eyre & Ferguson 2009), which is similar to the average carbon mineralization reported for permeable shelf sands ($\sim 5\text{--}10 \text{ mol C m}^{-2} \text{ y}^{-1}$). Denitrification rates that appear to be uncoupled from sediment organic content may be a consequence of the quality of the organic matter and should not lead to the conclusion that coupled nitrification-denitrification here is unimportant.

The highest denitrification in the shelf may be reached between the highly oxidized mixed sands in the inner shelf and the deeper accumulating sediments of the upper slope (Figure 4). In this denitrification zone, the sediments may still be relatively permeable, but their higher organic matter content causes larger redox oscillations that promote coupled nitrification-denitrification. Because of the rapid advective supply of substrates and ensuing redox changes, shelf sands can respond instantly to organic matter input with enhanced denitrification, as supported by an immediate 16-fold N_2 release after phytodetritus addition to flushed sands (Gihring et al. 2009). Consequently, the N_2 release from the sediment is correlated to pore-water flow, increasing from $0.12 \text{ mmol N m}^{-2} \text{ d}^{-1}$ under diffusion-limited transport to $0.87 \text{ mmol N m}^{-2} \text{ d}^{-1}$ under advective transport in Gulf of Mexico sublittoral sands (Gihring et al. 2010).

This dependency of denitrification rate on flow and advective substrate supply has to be considered when assessing published denitrification rates for permeable shelf sands. Reported denitrification rates range from $0.02\text{--}0.03 \text{ mmol N m}^{-2} \text{ d}^{-1}$ on the Georgia continental shelf (Vance-Harris & Ingall 2005) and $0.31 \text{ mmol N m}^{-2} \text{ d}^{-1}$ in the North Sea (Gao et al. 2010) to $5.44 \text{ mmol N m}^{-2} \text{ d}^{-1}$ at 17-m water depth on the Mid-Atlantic Bight sandy shelf (Laursen & Seitzinger 2002). This Mid-Atlantic Bight rate is among the highest recorded in a marine environment, emphasizing the importance of permeable shelf sands as sites for denitrification. Gao et al. (2010) reported denitrification rates of similar magnitude ($4.6 \text{ mmol N m}^{-2} \text{ d}^{-1}$) in North Sea intertidal sands, where denitrification occurred under oxic conditions. Rao et al. (2007) also observed such aerobic denitrification in oxic South Atlantic Bight sands, suggesting that denitrifying bacteria in permeable sands may have adapted to the frequent redox changes associated with the moving pore-water flow patterns.



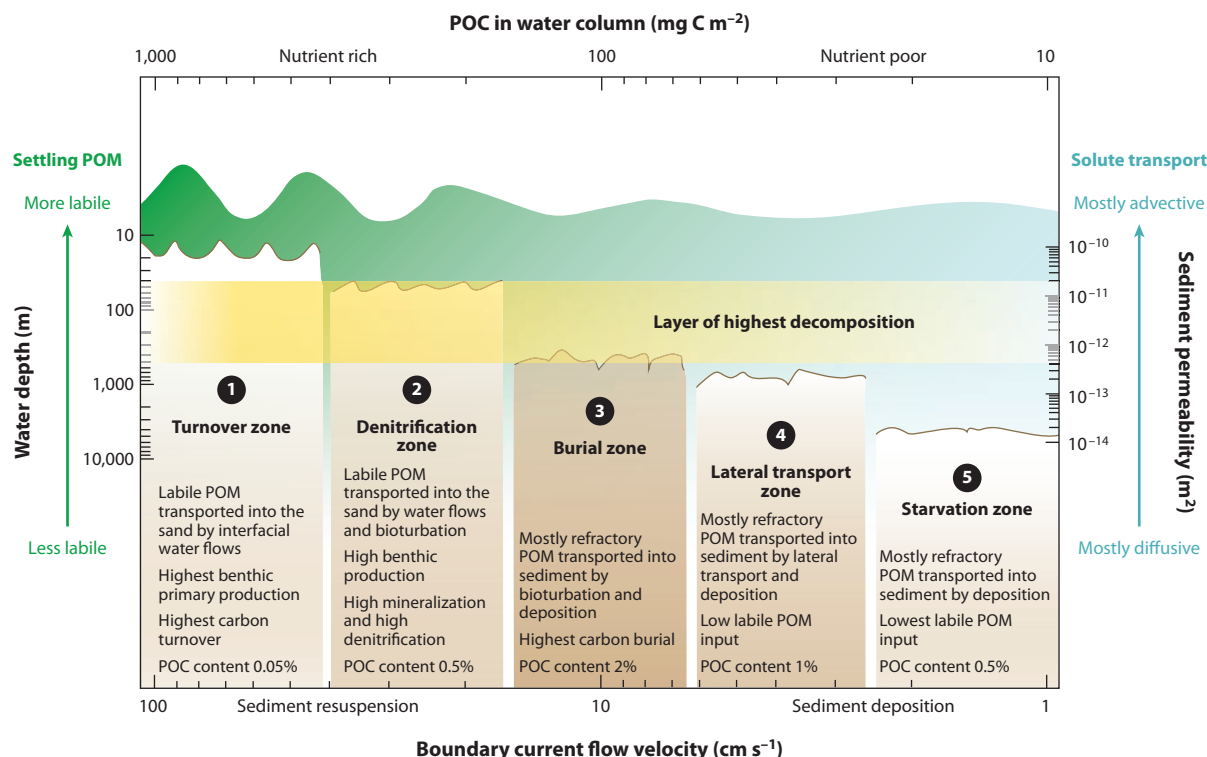


Figure 4

Decomposition activity as depth decreases. In shallower waters, the layer of highest decomposition activity gradually moves into the sediment. ① In the shallow shelf, wave and strong bottom currents cause frequent resuspension, which keeps the sediment highly permeable. Fresh organic matter from the highly productive water column and sediment surface is transported deep into the sands by strong advective pore-water flows. No organic matter is buried, owing to rapid turnover promoted by the interfacial flows of oxygen-saturated water. ② Sedimentary denitrification peaks in the zone between the shallow, highly oxidized sand beds and the depocenter in the deeper shelf slope with low oxygen content. In this zone, sporadic resuspension keeps the sediment sufficiently permeable to allow advective pore-water transport. The combined production of the water column and sediment reaches maximum rates, and the weaker bottom currents allow occasional settling of organic particles and the growth of abundant macrofauna. Hydrodynamic and biological filtering and mixing mechanisms combine, which results in high decomposition rates.

③ The depocenter in the shelf slope receives mainly refractory organic material, and the slower bottom currents allow the deposition of fine particles, causing low sediment permeability. The resulting lack of advective oxidation and reduced bioturbation cause the highest burial rates. ④ Below the depocenter, particulate organic matter (POM) input gradually decreases, and the sediment for mineralization becomes less important. Downslope POM transport becomes more important. ⑤ Bacterial growth on sinking POM peaks at 500-m water depth, where the greatest breakup of particles also occurs. Only 2–4% of surface-water primary production reaches the deep seafloor, minimizing the contribution of the sediment for its mineralization. Additional abbreviation: POC, particulate organic carbon. Adapted from Huettel & Rusch (2000).

The highest denitrification rates in sandy shelf sediments occur in tropical environments, where microenvironments within the porous carbonate grains can further enhance biogeochemical reactions (Santos et al. 2012a). Denitrification in these areas is typically in the range of 1–2 mmol N m⁻² d⁻¹, but the annual deposition of coral spawning products leads to rates reaching 11.5 mmol N m⁻² d⁻¹ (Eyre et al. 2008). In these carbonate sands, approximately 75% of the nitrogen mineralized is denitrified, emphasizing the role of coupled nitrification-denitrification in the high nitrogen removal rates of tropical sandy shelves (Santos et al. 2012a). In Mid-Atlantic Bight sands, denitrification accounts for approximately 13% of total sedimentary carbon mineralization

(Laursen & Seitzinger 2002), revealing that this process plays a significant role in shelf carbon cycling. Microbial anammox, which can also remove nitrogen from marine systems by shunting nitrogen directly from NH_4^+ to N_2 , has been considered less important in permeable sands (Amano et al. 2007, Vance-Harris & Ingall 2005). This view has been challenged by recent research that suggests that anammox may play a significant role in the removal of nitrogen from permeable sediments, especially in cold environments (Canion et al. 2013, Kostka et al. 2008).

11. PERMEABLE SHELF SANDS IN THE GLOBAL BIOGEOCHEMICAL CYCLES

Jahnke (2010) classified continental margins into two major groups: (a) slope-dominated systems with narrow shelves, where the majority of primary production occurs seaward of the shelf break, fed by nutrient-rich upwelling, and (b) shelf-dominated systems with broad, shallow shelves, where the majority of primary production occurs shoreward of the shelf break. Approximately 80% of global continental margins are shelf-dominated systems, and the relatively flat topography of these trailing-edge coasts and the relatively low associated river-flow velocities (Inman & Nordstrom 1971) limit sediment input from land, which would reduce the permeability of the coastal sand bed.

The characteristics of these shelf sands and their functioning in the cycles of matter can be seen as the product of energy gradients that culminate in the inner shelf: chemically bound energy from land, products of photosynthesis, and hydrodynamic mixing (**Figure 5**). Organic matter and nutrient discharge to the coastal zones through rivers, surface runoff, and groundwater seepage generate a gradient of chemically bound energy that increases to maximum values on the inner shelf. Intense pelagic primary production exploits this nutrient gradient, as reflected in steep increases of chlorophyll concentrations toward the coast. Irradiation energy conversion into biomass is enhanced by light penetration to the shallow shelf bottom, where benthic photosynthesis profiting from sedimentary nutrient release generates organic carbon at rates rivaling those of pelagic production, thereby doubling carbon fixation in the inner shelf. The gradual decreases in water depth toward the coast and ensuing compression of waves, tides, and wind-forced and geostrophic currents convert potential into kinetic energy, resulting in increased turbulence, mixing, bottom shear, and heat. Through their influence on grain size spectrum and sorting, the gradients in currents and bottom shear define the granulometric characteristics of the sand bed and its permeability and filtration rates. Sediments thus become coarser and more permeable closer to the coasts, and the associated increase in benthic filtration combines with the increase in primary production boosted by nutrient input and hydrodynamic mixing.

In contrast to depositional environments, where the organisms of muddy seabeds consume decaying material settling out of the photic zone (first-order decay constants on the order of $0.01\text{--}0.5\text{ y}^{-1}$; Boudreau 1997), permeable sand beds of the inner shelf decompose fresh organic matter filtered from the water column and produced in the photosynthetically active sediment surface layer (decay constants of $0.05\text{--}3.5\text{ y}^{-1}$). As a result of the energy maximum in the inner shelf and the increased mineralization efficiency in the oxygenated permeable shelf beds, benthic respiration rates (R) increase exponentially with decreasing water depth (d) according to the empirical relationship $R = 32.1 \times e^{-0.0077 \times d}$ (for depth $< 300\text{ m}$, where R is in millimoles per square meter per day and d is in meters) (Middelburg et al. 2004). Applying this relationship to the surface area of the shelf (depth $< 200\text{ m}$, $23.9 \times 10^6\text{ km}^2$) results in a shelf sediment respiration of 166 Tmol C y^{-1} (Middelburg et al. 2004), consistent with previous global estimates of $150\text{--}160\text{ Tmol C y}^{-1}$ (Jørgensen 1983, Wollast 1998). Assuming a respiration rate of $15\text{--}45\text{ mmol C m}^{-2}\text{ d}^{-1}$ —as measured in permeable sand sediments of the Mid-Atlantic Shelf (Reimers et al. 2004), South Atlantic Bight (Marinelli et al. 1998), and North Sea (Janssen et al.



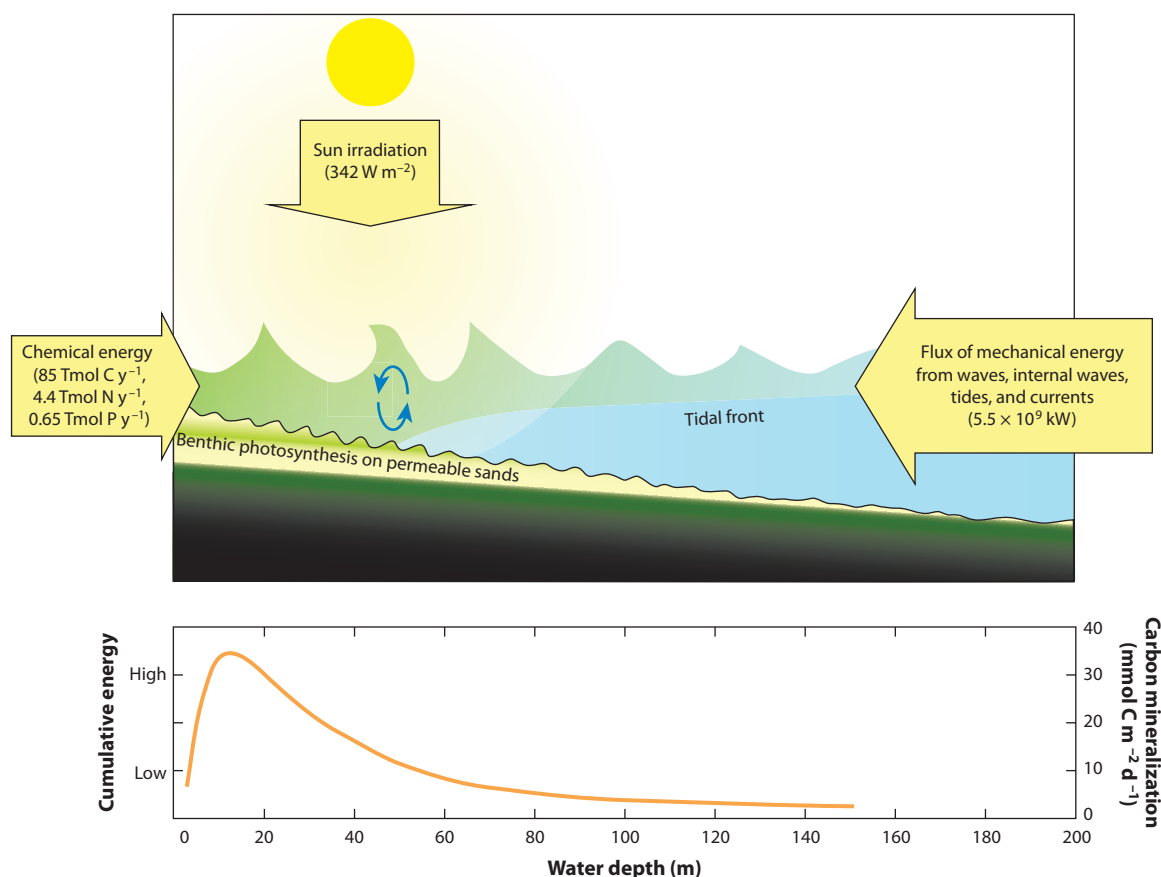


Figure 5

Energy inputs in the shallow shelf. Chemical energy from land (in the form of organic matter), photosynthetic conversion of energy from sun irradiation, and kinetic energy from waves, tides, and currents culminate in the shallow shelf, making a maximum of energy available for pelagic and benthic productivity in the coastal zone, where permeable sediments cover the seafloor. Chemical energy data are from Ducklow & McCallister (2005), carbon mineralization data are from Middelburg & Soetaert (2005), and irradiation and mechanical energy data are from Inman & Jenkins (2005).

2005b)—and extrapolating this conservative flux to the global inner-shelf area (depth <25 m, 7.4×10^6 km²) results in a global respiration rate in permeable inner-shelf sands of 41–121 Tmol C y⁻¹, suggesting that 24–73% of the shelf benthic respiration is associated with permeable sediments (Table 3). Jahnke's (2010) estimate of 920 Tmol C y⁻¹ for global shelf primary production indicates that the permeable sediments can recycle 4–13% of this production. The rapid decomposition of organic matter in the sands and efficient equilibration with the atmosphere lead to CO₂ outgassing and make the shallow shelf a source of CO₂ (Liu et al. 2010a).

The tight coupling between carbon mineralization and nitrogen removal in the shelf influences primary productivity and ultimately atmospheric CO₂ levels (Gruber & Galloway 2008). Continental margin sediments account for ~44% of total global denitrification (Seitzinger et al. 2006), and applying a conservative denitrification rate of 1 mmol N m⁻² d⁻¹ (Laursen & Seitzinger 2002) to the global inner-shelf area results in 2.7 Tmol N y⁻¹ that could potentially be released from permeable shelf sands. Seitzinger et al.'s (2006) estimate for denitrification in continental shelf

Table 3 Calculated estimates of the contribution of permeable shelf sands to global shelf carbon mineralization and denitrification

Descriptor	Value or range	Reference(s)
Global shelf area (depth <200 m)	$23.9 \times 10^6 \text{ km}^2$	Amante & Eakins 2009
Respiration rate in global shelf sediment	$20\text{--}24 \text{ mmol C m}^{-2} \text{ d}^{-1}$	Middelburg et al. 2004
Global shelf sediment respiration	$150\text{--}170 \text{ Tmol C y}^{-1}$	Jørgensen 1983, Middelburg et al. 2004, Wollast 1998
Assumed global permeable sands respiration rate	$15\text{--}45 \text{ mmol C m}^{-2} \text{ d}^{-1}$	Janssen et al. 2005b, Marinelli et al. 1998, Reimers et al. 2004
Global inner shelf area with permeable sands (depth <25 m)	$7.4 \times 10^6 \text{ km}^2$	Amante & Eakins 2009
Global respiration rate in permeable inner-shelf sands	$41\text{--}121 \text{ Tmol C y}^{-1}$	Calculated based on numbers in this table
Permeable sand contribution to global shelf sediment respiration	24–73%	
Global shelf primary production	$920 \text{ Tmol C y}^{-1}$	Jahnke 2010
Potential recycling of global shelf primary production in permeable shelf sands	4–13%	Calculated based on numbers in this table
Denitrification in global shelf sediments (depth <200 m)	18 Tmol N y^{-1}	Seitzinger et al. 2006
Assumed global denitrification rate in global shelf permeable sands	$1 \text{ mmol N m}^{-2} \text{ d}^{-1}$	Laursen & Seitzinger 2002
Denitrification in global shelf permeable sands	$2.7 \text{ Tmol N y}^{-1}$	Calculated based on numbers in this table
Permeable sand contribution to global shelf sediment denitrification	15%	

sediments (depth <200 m, 18 Tmol N y^{-1}) suggests that permeable sediments of the inner shelf (depth <25 m) contribute approximately 15% of this nitrogen removal.

Human activities fundamentally change the functioning of the shelf by causing coastal eutrophication, increases in sea level and water temperature, and enhanced storm activity. Continental margins as a whole may have already changed from a net source of CO_2 to a net sink of CO_2 (Liu et al. 2010a). Increases in nutrient and sediment input in the inner shelf create shading that reduces benthic primary production; consequently, oxygen production and its advective transport into the sediment decrease, lowering aerobic degradation processes and promoting organic matter burial. Increased anaerobic degradation using sulfate as an electron acceptor produces sulfide that can inhibit nitrification and therefore denitrification and nitrogen removal from the shelf (Joye & Hollibaugh 1995). Enhanced organic matter burial and the associated increases in sedimentary bacterial biomass over time lower sediment permeability, reducing advective flushing and closing a feedback loop. If enhanced storm activity cannot offset this process, this feedback may transform sands into anoxic muddy sands, as has occurred in heavily impacted estuarine environments such as Chesapeake Bay (Dauer et al. 2000). A partly clogged coastal biocatalytic sand filter would reduce water quality, thereby impacting coastal ecosystems, fisheries, and the recreational value of the coast.

Owing to the lack of direct measurements, we still do not have a good understanding of the functioning of permeable sands and their role in ocean biogeochemical cycling. The data presented here suggest that permeable shelf sands play an important role in the global cycles of matter, emphasizing the need for further research focusing on this dynamic coastal environment.

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