Biogeosciences
Open Access
Discussions

Stimulation of microbial nitrogen cycling in aquatic ecosystems by benthic macrofauna: mechanisms and environmental implications

P. Stief[1,2]

[1]Max Planck Institute for Marine Microbiology, Microsensor Group, Bremen, Germany
[2]University of Southern Denmark, Institute of Biology, NordCEE, Odense, Denmark

Received: 1 July 2013 – Accepted: 2 July 2013 – Published: 15 July 2013

Correspondence to: P. Stief (peterstief@biology.sdu.dk)

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

BGD

10, 11785–11824, 2013

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Title Page

Abstract | Introduction
Conclusions | References
Tables | Figures

◄ | ►
◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Invertebrate animals that live at the bottom of aquatic ecosystems (i.e., benthic macro-fauna) are important mediators between nutrients in the water column and microbes in the benthos. The presence of benthic macrofauna stimulates microbial nutrient dy-namics through different types of animal–microbe interactions, which potentially affect the trophic status of aquatic ecosystems. This review contrasts three types of animal–microbe interactions in the benthos of aquatic ecosystems: (i) ecosystem engineering, (ii) grazing, and (iii) symbiosis. Their specific contributions to the turnover of fixed ni-trogen (mainly nitrate and ammonium) and the emission of the greenhouse gas nitrous oxide are evaluated.

Published data indicate that ecosystem engineering by sediment-burrowing macro-fauna stimulates benthic nitrification and denitrification, which together allows fixed ni-trogen removal. However, the release of ammonium from sediments often is enhanced even more than the sedimentary uptake of nitrate. Ecosystem engineering by reef-building macrofauna increases nitrogen retention and ammonium concentrations in shallow aquatic ecosystems, but allows organic nitrogen removal through harvesting. Grazing by macrofauna on benthic microbes apparently has small or neutral effects on nitrogen cycling. Animal-microbe symbioses provide abundant and distinct benthic compartments for a multitude of nitrogen-cycle pathways. Recent studies revealed that ecosystem engineering, grazing, and symbioses of benthic macrofauna significantly enhance nitrous oxide emission from shallow aquatic ecosystems.

The beneficial effect of benthic macrofauna on fixed nitrogen removal through cou-pled nitrification–denitrification can thus be offset by the concurrent release of (i) am-monium that stimulates aquatic primary production and (ii) nitrous oxide that con-tributes to global warming. Overall, benthic macrofauna intensifies the coupling be-tween benthos, pelagial, and atmosphere through enhanced turnover and transport of nitrogen.

1   Introduction

Sediments of lakes, streams, and marine coasts are major compartments of the microbial nitrogen cycle (N-cycle) in aquatic ecosystems (Thamdrup and Dalsgaard, 2008). Much of the particulate organic nitrogen (PON) that settles onto sediments is rapidly converted to ammonium (Fig. 1). At the oxic sediment surface, ammonium is oxidized to nitrite and further to nitrate by two functional groups of nitrifying bacteria: ammonia oxidizers and nitrite oxidizers. Additionally, ammonia oxidation is mediated by archaea that occur ubiquitously in aquatic sediments. Nitrite and nitrate produced by nitrifiers may both diffuse partially into the water column and partially into anoxic sediment layers where they are reduced through three different nitrogen-cycle pathways to either dinitrogen (i.e., by denitrification and anaerobic ammonium oxidation, anammox) or ammonium (i.e., by dissimilatory nitrate reduction to ammonium, DNRA) by facultatively or strictly anaerobic bacteria. Nitrate may also directly diffuse from the water column into anoxic sediment layers where it is reduced to either dinitrogen or ammonium. Thus, benthic mineralization of PON and microbial nitrogen conversions eventually produce dissolved inorganic nitrogen (DIN) that partially diffuses back into the water column where it fuels primary production and is partially converted to dinitrogen that is biologically unavailable to most organisms and thus largely leaves the ecosystem. Specifically, nitrification, denitrification, and anammox in the sediment contribute to fixed nitrogen removal from aquatic ecosystems, whereas DNRA only recycles fixed nitrogen.

Current concerns arise from excess fixed nitrogen in the environment due to (i) extensive use of synthetic fertilizers in agriculture with subsequent leaching of nitrate into water bodies and (ii) fossil fuel burning followed by atmospheric nitrogen deposition (Gruber and Galloway, 2008; Feuchtmayr et al., 2009). Excess nitrate and ammonium in aquatic ecosystems contribute to eutrophication with detrimental consequences for the environment, such as algal blooms, oxygen depletion, habitat degradation, and loss of biodiversity (Nixon, 1995; Rabalais, 2002; Feuchtmayr et al., 2009; Howarth et al., 2011). The microbial N-cycle also produces toxic compounds (e.g., nitrite, ammonia)

and a potent greenhouse gas (i.e., nitrous oxide) at rates often directly proportional to DIN concentrations in the water column (Seitzinger and Kroeze, 1998). Environmental problems arising from excess fixed nitrogen pertain to both freshwater and coastal marine ecosystems and call for management strategies that reduce the sources of fixed nitrogen and/or increase the capacity of fixed nitrogen removal.

Benthic microbes share their habitat with a large diversity of invertebrate animals. In fact, some of the abundant benthic macrofauna species act as important mediators between N-cycle bacteria in the benthos and fixed nitrogen in the water column. The burrowing activity by macrofauna in the sediment extends the oxic–anoxic interface to deeper sediment layers (Laverock et al., 2011); and the ventilation activity by macrofauna inside the burrows tremendously enhances the transport of solutes and suspended particles between water column and sediment (Aller and Aller, 1998). By such bioturbation activities (i.e., particle reworking and burrow ventilation, Kristensen et al., 2012), macrofauna may stimulate microbial nitrogen cycling which is particularly intense at oxic–anoxic interfaces (Thamdrup, 2012) and the transport of DIN and PON between the sediment and the water column (Kristensen and Kostka, 2005). These stimulatory effects by macrofauna potentially remove fixed nitrogen from aquatic ecosystems through the sequential action of ammonification, nitrification, and denitrification and/or anammox (Fig. 1). However, recent findings reveal that microbial nitrous oxide production can be directly associated with many freshwater and marine macrofauna species and their burrows in the sediment, which potentially increases total nitrous oxide emission rates from aquatic ecosystems (Stief et al., 2009; Heisterkamp et al., 2010).

In the last two decades, some of the mechanisms of macrofauna-induced stimulation of benthic nitrogen cycling and the microbes affected by this stimulation have been unraveled by making use of methodical advancements. Non-invasive microsensors were used in burrows, guts, and exoskeletal biofilms of benthic macrofauna to uncover the microscale oxygen and DIN dynamics in these animal-associated compartments (Stief and de Beer, 2006; Stief and Eller, 2006; Stief et al., 2009; Heisterkamp

et al., 2013). Additionally, the cultivation-independent community analysis of bacteria allowed to specifically detect bacteria involved in nitrogen cycling directly in the environment, for instance, by using fluorescence in situ hybridization targeting nitrifying bacteria (Altmann et al., 2004; Stief and de Beer, 2006) or by sequencing of phylogenetic marker genes or functional genes of nitrifying and denitrifying bacteria (Dollhopf et al., 2005; Satoh et al., 2007; Stief et al., 2009; Svenningsen et al., 2012; Gilbertson et al., 2012).

This review article evaluates in which way the presence of benthic macrofauna mitigates or aggravates environmental problems caused by excess fixed nitrogen in aquatic ecosystems. Three different types of animal–microbe interactions (and their transition forms) are discussed with respect to mechanism, representative examples, and ecosystem-level impact on nitrogen cycling: (i) ecosystem engineering, (ii) grazing, and (iii) symbiosis. Particular attention is paid to the recent discovery that significant production of nitrous oxide is directly or indirectly associated with benthic macrofauna.

2 Interactions between benthic macrofauna and nitrogen-cycle bacteria

2.1 Ecosystem engineering

2.1.1 Sediment infauna

Many benthic macrofauna species construct sedimentary burrows that serve as protective retreats, but which also create a unique microenvironment for sediment bacteria (Fig. 2a). Burrowing macrofauna thereby alter the resource supply to sediment bacteria and thus act as ecosystem engineers (Jones et al., 1994; Meysman et al., 2006). In the burrow microenvironment, bacteria face (i) subsurface extensions of the oxic–anoxic interface, (ii) rich deposits of labile organic matter in the burrow wall, (iii) oscillating oxygen and DIN concentrations in the burrow lumen due to periodic ventilation activity of the animal, and (iv) pulses of ammonium excreted by the animal into the bur-

row lumen (Gardner et al., 1983; Kristensen et al., 1991; Papaspyrou et al., 2005; Stief and de Beer, 2006). This sequential or simultaneous presence of electron acceptors and donors in high concentration turns macrofauna burrows into "hot spots" of both aerobic and anaerobic microbial processes, such as the various N-cycle pathways.

Outstanding taxonomic groups of benthic infauna that act as ecosystem engineers are chironomids, tubificids, and burrowing mayfly larvae in freshwater sediments as well as polychaetes, crustaceans, and mollusks in coastal marine sediments. Density-dependent stimulations of N-cycle pathways and DIN fluxes are, for instance, reported for the insect *Chironomus plumosus* (Pelegri and Blackburn, 1996; Svensson, 1997, 1998; Stief et al., 2009), the oligochaete *Tubifex tubifex* (Svensson et al., 2001), the ragworm *Nereis* sp. (Bartoli et al., 2000), the mud shrimp *Corophium* sp. (Pelegri and Blackburn, 1994), and a number of other burrowing crustaceans (Webb and Eyre, 2004; D'Andrea and DeWitt, 2009; Jordan et al., 2009). Density-dependent stimulation of nitrogen cycling is not generally observed though (e.g., Dunn et al., 2009). Often, animal species with high ventilation rates have strong per capita impacts on N-cycle pathways and DIN fluxes, especially when occurring at high in situ densities (Mayer et al., 1995; Svensson and Leonardson, 1996; Svensson et al., 2001; Nielsen et al., 2004). The highly abundant chironomid larvae, for instance, irrigate their burrows intermittently (Lewandowski et al., 2007; Roskosch et al., 2010) and thereby significantly stimulate sedimentary nitrification and denitrification and consequently the exchange of DIN across the sediment–water interface in lakes (Pelegri and Blackburn, 1996; Svensson, 1997, 1998; Stief and Hölker, 2006; Stief et al., 2009).

Stimulation of nitrification activity inside macrofauna burrows results from the enhanced availability of oxygen, ammonium, and carbon dioxide due to ventilation, excretion, and respiration activities of the inhabiting animals (Mayer et al., 1995; Satoh et al., 2007). Consequently, the abundance of nitrifying bacteria in the burrow walls is significantly higher than in the sediment surrounding the burrows (Satoh et al., 2007). Stimulation of denitrification activity inside macrofauna burrows results from the advective transport of oxygen and nitrate into the burrows during ventilation periods, followed

by oxygen depletion and anaerobic nitrate consumption during resting periods of the animals (Svensson, 1998). Additionally, denitrification activity inside burrows is coupled to nitrate and nitrite production by nitrification in the burrow walls, leading to a high relative contribution of coupled nitrification–denitrification to total denitrification (Howe et al., 2004). The demand of denitrifying bacteria for electron donors is met by the labile organic matter that the burrow walls are enriched with (Stief, 2007). Recently, the use of microsensors directly in the burrow lumen and the burrow wall has confirmed both the oscillating oxygen and DIN concentrations in ventilated burrows (Stief and de Beer, 2006; Stief et al., 2009) and the enhanced rates of nitrification and denitrification in the burrow walls (Nielsen et al., 2004; Stief et al., 2004; Satoh et al., 2007).

The net result of ventilation-enhanced solute exchange between water column and sediment depends on the relative rates of organic matter mineralization, ammonium excretion, nitrification, and denitrification inside the burrows. Many burrowing macrofauna species enhance (i) the net efflux of ammonium because rates of organic matter mineralization and ammonium excretion exceed the rate of nitrification (e.g., Pelegri and Blackburn, 1995; Svensson, 1997; Hansen and Kristensen, 1998; Stief and Hölker, 2006; Lewandowski et al., 2007) and (ii) the net influx of nitrate because the rate of denitrification exceeds the rate of nitrification (e.g., Pelegri and Blackburn, 1996; Nizzoli et al., 2007). However, ventilation-enhanced net efflux of nitrate by burrowing macrofauna is sometimes observed too (Christensen et al., 2000; D'Andrea and DeWitt, 2009). Additionally, several freshwater species enhance the efflux of nitrous oxide in a density-dependent manner (Svensson, 1998; Stief et al., 2009; Stief and Schramm, 2010; Poulsen et al., 2013) (see below).

2.1.2 Sediment epifauna

Reef-building macrofauna species live in huge aggregations of individuals on top of soft and hard bottoms of shallow aquatic ecosystems and act as ecosystem engineers by altering the resource supply to other organisms (Jones et al., 1994; Markert et al., 2010) (Fig. 2b). In the reef structures, benthic microbes face (i) an extension of hard-

substrate colonization surfaces, (ii) changed flow conditions and sedimentation rates, (iii) an enrichment of organic matter and ammonium due to macrofaunal biodeposition and excretion, respectively, and (iv) changed light and oxygen conditions due to water clearance through filter feeding by the reef-building organisms. As a consequence, macrofaunal reefs significantly affect microbially-mediated nutrient dynamics in shallow aquatic ecosystems, including nitrogen cycling.

The world's largest biogenic reefs are the tropical coral reefs formed by colonial scleractinians (stony corals). Effects of reef-building macrofauna on the microbial N-cycle, however, are mainly reported for the bivalves *Crassostrea* sp. (oysters) and *Mytilus* sp. (blue mussels) in coastal marine ecosystems and *Dreissena* sp. (zebra mussels) in freshwater ecosystems. *Crassostrea* sp. (Dame et al., 1992; Gilbert et al., 1997; Souchu et al., 2001; Newell et al., 2002; Piehler and Smyth, 2011; Kellogg et al., 2013), *Mytilus* sp. (Prins and Smaal, 1994; Nizzoli et al., 2005; Stenton-Dozey et al., 2001), and *Dreissena* sp. (Gardner et al., 1995; Lavrentyev et al., 2000; Conroy et al., 2005; Bruesewitz et al., 2006, 2008; Svenningsen et al., 2012) have been shown to significantly affect benthic DIN fluxes. Additionally, *Crassostrea gigas* and *Dreissena polymorpha* have a very high potential for invading aquatic ecosystems, often with severe ecological and economic consequences (Pejchar and Mooney, 2009; Strayer, 2009; Higgins and Vander Zanden, 2010; Markert et al., 2010). On the other hand, *Crassostrea* sp. and *Mytilus* sp. are used in shellfish farming (Hatcher et al., 1994; Gilbert et al., 1997; Souchu et al., 2001; Nizzoli et al., 2005, 2006) and for ecosystem restoration by exploiting their high filter-feeding activity (Newell et al., 2005; Plutchak et al., 2010; Higgins et al., 2011, 2013; Carmichael et al., 2012; Kellogg et al., 2013).

Bivalve reefs stimulate microbial nitrogen cycling through a combination of several mechanisms that mostly function at the level of the collective of the reef builders. The vast abundance of individuals confers a particular strength to the reef's effects on benthic DIN fluxes in shallow and constrained water bodies. Bivalve shells represent a wealth of hard substrata for colonization by biofilm-forming microbes (Gutierrez et al., 2003), including nitrifying and denitrifying bacteria (Welsh and Castadelli, 2004;

Heisterkamp et al., 2013). Nitrifying bacteria living in shell biofilms are nourished by metabolic waste products, such as ammonium and carbon dioxide, excreted by the reef-building organisms (Dame et al., 1992; Newell et al., 2002; Plutchak et al., 2010). Denitrifying bacteria benefit from the enrichment of labile organic matter in the reef due to biodeposition of suspended particles (i.e., seston) as mediated by the reef builders (Newell et al., 2005; Piehler and Smyth, 2011; Kellogg et al., 2013). Biodeposition of seston results from the filter-feeding activity by the bivalves followed by the production and enhanced sedimentation of feces and pseudofeces. Sedimentation and biodeposition of seston are further facilitated by low-flow areas within the surface relief of the reef (Lenihan, 1999). The filter-feeding activity by the bivalves also reduces phytoplankton densities, which leads to higher light penetration into the water body (Dame et al., 1992; Souchu et al., 2001; Newell et al., 2002). Since abundance and activity of microphytobenthos increase with enhanced light intensities, near-bed oxygen concentrations tend to be higher (Lenihan, 1999) and potentially stimulate coupled nitrification–denitrification (Souchu et al., 2001; Newell et al., 2002). In contrast, extremely high rates of biodeposition in long-line mussel farms reduce oxygen availability and nitrification activity in the underlying sediments (Nizzoli et al., 2005, 2006; Carlsson et al., 2010). Fixed nitrogen removal from aquatic ecosystems via natural bivalve reefs or mussel farming is also achieved by harvesting the biomass (Newell et al., 2005; Higgins et al., 2011; Stadmark and Conley, 2011; Rose et al., 2012; Carmichael et al., 2012; Kellogg et al., 2013) or through predation by waterfowl (Hamilton et al., 1994).

2.2 Grazing

Benthic macrofauna species graze on bacteria by filter feeding, deposit feeding, and scraping of biofilms. Typically, the ingested bacteria are attached to sediment grains or detritus particles or they are embedded in a biofilm matrix. Macrofaunal bacterivory has the potential to decrease the abundance of N-cycle bacteria and thereby also the rates of nitrification and denitrification (Fig. 2c). The advent of cultivation-independent methods to study individual cells, populations, and communities of microbes has made

it possible to specifically target phylogenetic or functional groups of microbes directly in environmental samples. The abundance of bacteria involved in nitrification and denitrification, potentially reduced by macrofaunal grazing, can now be determined at the level of individual cells by fluorescence in situ hybridization (Altmann et al., 2004) and at the level of gene abundance by quantitative PCR targeting phylogenetic marker genes or functional genes (Dollhopf et al., 2005; Satoh et al., 2007; Gilbertson et al., 2012).

Isotopic evidence for macrofaunal grazing on bacteria exists for freshwater and marine species (Levin and Michener, 2002; Deines et al., 2007; Pascal et al., 2008). The bacterial diet provides, however, only a minor fraction of the carbon demand of benthic macrofauna (Kemp, 1987; Johnson et al., 1989; Goedkoop and Johnson, 1994). In turn, the grazing effect on total sediment bacteria is quantitatively not important because benthic macrofauna species consume only a small fraction of the total bacterial production (Johnson et al., 1989; Van de Bund et al., 1994; Pascal et al., 2008). Rapid regrowth of bacterial populations apparently compensates for the losses caused by macrofaunal bacterivory (Van de Bund et al., 1994; Plante and Wilde, 2001). Additionally, bacterivorous macrofauna species may even promote the regrowth of sediment bacteria through ecosystem engineering (see above).

Persistent grazing effects on sediment bacteria only exist for bacterial groups that are efficiently eliminated by bacteriolysis in the animal gut and/or for those that show low growth rates in their benthic environment (Plante and Mayer, 1994; Altmann et al., 2004). Nitrifying bacteria belong to the latter group and their abundance is indeed reduced in the deposit-feeding layer of *Chironomus riparius* larvae (Altmann et al., 2004; Stief and de Beer, 2006). In the ventilation layer of the larvae, however, the total nitrifier abundance is higher than in control sediments, probably due to low grazing pressure and/or favorable growth conditions (Stief and de Beer, 2006). Thus, the direct effect of *C. riparius* larvae on the abundance of nitrifying bacteria due to grazing is partially offset by indirect effects due to ecosystem engineering. In fact, nitrification rates were lower in the deposit-feeding layer of the larvae, while the total DIN fluxes between water column and sediment were not significantly different (Altmann et al., 2004). Several

marine macrofauna species affect both the abundance ratio of archaeal to bacterial ammonia oxidizers and nitrification rates, but not the overall abundance of ammonia oxidizers (Gilbertson et al., 2012). Hence, grazing (probably together with ecosystem engineering) may also exclusively alter the community structure of ammonia oxidizers and thereby affect nitrification rates. Persistent grazing effects on denitrifying bacteria have so far not been documented for aquatic sediments. It can be expected that this functional group of bacteria will experience only a weak grazing pressure by macrofauna due to their subsurface occurrence and their generally high growth rates, but experimental evidence is currently lacking. Additionally, it has been shown that denitrifying bacteria survive the gut passage when ingested by benthic macrofauna (Stief et al., 2009). In agreement with this finding, sediments inhabited or non-inhabited by *C. plumosus* larvae did not differ in the abundance of functional genes of dissimilatory nitrate reduction and denitrification (Poulsen et al., 2013).

2.3 Symbiosis

The body of benthic macrofauna features permanent or transient habitats for bacteria and other microbes. Hard body surfaces may carry microbial biofilms, soft tissues may host cellular and extracellular symbionts, and guts constitute transient habitats for ingested bacteria or permanent habitats for symbionts of the gut wall (Fig. 2d). While such intimate organismic associations can loosely be termed symbioses (as is done here), the functional relationship between the macrofaunal and the microbial partners may in reality range from parasitism via commensalism to symbiosis. Very often, however, the type of functional relationship is not known and additionally smooth transitions exist between the different types. This review covers intimate associations of benthic macrofauna and N-cycle bacteria located in exoskeletal biofilms, gut contents, and the soft tissues of the animal (Fig. 2d). As a common trait of these associations, the microbial metabolism is mainly controlled by the substrates, nutrients, and microenvironmental conditions provided by the animal host (McFall-Ngai et al., 2013). Nitrogen

cycling mediated by symbionts of benthic macrofauna is thus partially uncoupled from the ambient supply of DIN and oxygen.

2.3.1 Exoskeletal biofilms

Benthic macrofauna with a hard body surface (e.g., a chitinous exoskeleton or a calcareous shell) are often colonized by microorganisms organized in biofilms (Wahl et al., 2012). Usually, these exoskeletal biofilms develop better in epifaunal species, such as reef-building bivalves, because of lower abrasion forces in the water column than in the sediment. Aside from mollusks (e.g., bivalves and gastropods), higher crustaceans and ascidians are reported to carry rich biofilms on their body surface (Heisterkamp et al., 2010). Exoskeletal biofilms of a number of marine species harbor nitrifying bacteria that are nourished by ammonium and carbon dioxide excreted by the animal host (Welsh and Castadelli, 2004; Welsh et al., 2009). The nitrification activities associated with abundant macrofauna species contribute to overall benthic nitrification rates aided by the efficient solute exchange between the biofilms and the ambient water (Welsh and Castadelli, 2004). Additionally, the shell biofilms of freshwater and marine mollusks produce substantial amounts of nitrous oxide via both nitrification and denitrification (Svenningsen et al., 2012; Heisterkamp et al., 2013) (see below).

2.3.2 Gut contents

Bacteria ingested by macrofauna are not necessarily digested and may in fact survive and remain metabolically active during the gut passage (Plante and Mayer, 1994). Furthermore, the gut microenvironment may induce metabolic pathways of the bacteria that are not active in their natural environment. As shown by microsensor measurements, the gut interior of many species is anoxic (Plante and Jumars, 1992; Stief and Eller, 2006; Stief et al., 2009), which even applies to relatively small marine zooplankton (Tang et al., 2011). Bacteria that normally live in oxic environments will thus experience a shift from oxic to anoxic conditions when ingested by filter- or deposit-feeding

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

macrofauna. This oxic-anoxic shift induces denitrification activity in facultatively anaerobic bacteria which then start producing nitrous oxide and dinitrogen, gases that are efficiently emitted from the gut and the animal (Stief et al., 2009). Nitrate obviously enters the gut when water-soaked food particles are ingested (Stief et al., 2010). Not all macrofauna species emit nitrous oxide though, some because they are predators and only ingest few bacteria (Stief and Schramm, 2010), while others do not emit nitrous oxide because of bacteriolytic activities in the gut (Plante and Mayer, 1994; Heisterkamp et al., 2010).

2.3.3 Soft tissues

Sponges are engaged in symbioses with diverse microbes (Hentschel et al., 2006; Fiore et al., 2010; Webster and Taylor, 2012). The environmental importance of sponge-microbe symbioses is due to the often high coverage of benthic habitats with sponges and their ability to process large volumes of ambient water. The periodic ventilation activity of sponges also causes dynamic changes between oxic and anoxic conditions inside the tissues (Schläppy et al., 2007, 2010b; Hoffmann et al., 2008). Consequently, both aerobic and anaerobic N-cycle pathways can be active in the same host organism in different body sections or at different times (Fiore et al., 2010). Some of the bacterial symbionts of sponges fix dinitrogen and supply the host and possibly the nutrient-poor environment with fixed nitrogen (Weisz et al., 2007; Fiore et al., 2012). Several sponge species exhibit nitrification activity due to symbiotic ammonia-oxidizing Archaea and Bacteria that obviously benefit from ammonium and carbon dioxide excreted by the sponge (Jimenez and Ribes, 2007; Bayer et al., 2008; Hoffmann et al., 2009; Schläppy et al., 2010a; Radax et al., 2012a). Consequently, nitrate excretion has been observed in the sponge *Aplysina aerophoba*, albeit at rates considerably lower than ammonium excretion (Bayer et al., 2008). In contrast, the sponge *Geodia barretti* constitutes a nitrate sink due to its high denitrification and anammox activities (Hoffmann et al., 2009). Additionally, this sponge harbors active ammonia-oxidizing Archaea and Bacteria as demonstrated by metatranscriptomics (Radax et al., 2012b). In

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

coastal marine ecosystems with high sponge cover, the extrapolated rates of sponge-mediated N-cycle pathways rival those measured in ambient sediments (Jimenez and Ribes, 2007; Hoffmann et al., 2009).

Nitrate reduction activity is also associated with marine tubeworms and nematodes, but the extent of their nitrate exchange with the water column is currently not known. In the trophosome of the tubeworm *Riftia pachyptila*, intracellular symbionts reduce nitrate to nitrite and/or ammonium, which may serve respiratory or assimilatory purposes (Hentschel and Felbeck, 1993; Girguis et al., 2000). For two marine nematode species, nitrate reduction to nitrite mediated by symbionts attached to the worms' cuticle was demonstrated (Hentschel et al., 1999). It was speculated that such ectosymbionts associated with the marine nematode *Robbea* sp. use nitrate in the absence of oxygen to oxidize sulfide (Bayer et al., 2009). These forms of symbiosis-derived nitrate reduction, if widespread in nematodes, could be environmentally important because of the high abundance of nematodes in coastal marine sediments. Dedicated research is needed to quantify the potential contribution of benthic nematodes to microbial nitrogen cycling.

Many more symbiotic associations exist that involve N-conversions by the bacterial symbiont and N-transfer to the host animal, such as bacterial nitrogen fixation in shipworms and bivalves (Lechene et al., 2007) and corals (Fiore et al., 2010), archaeal ammonia oxidation in colonial ascidians (Martinez-Garcia et al., 2008), and bacterial regeneration of nitrogenous waste products in leeches (Kikuchi et al., 2009). The environmental significance of these highly specific symbioses is probably low because of the efficient transfer of substrates and nutrients between the symbiotic partners and because in many cases the bacterial symbionts are phagocytosed by the host animal.

3   Ecosystem-level impact of animal–microbe interactions

3.1   Theoretical considerations

The effects of benthic macrofauna on the aquatic N-cycle are often studied in the context of excess fixed nitrogen in aquatic ecosystems. Many of these studies suggestively link the stimulation of benthic nitrogen cycling by macrofauna to ecosystem-level fixed nitrogen removal. A factual reduction of DIN concentrations in the water column, the key criterion of ecosystem-level fixed nitrogen removal, will limit primary production and slow down or even reverse the eutrophication process. Fixed nitrogen removal from the aquatic ecosystems occurs through (i) long-term PON burial in deep sediment, (ii) dinitrogen emission to the atmosphere, (iii) feeding on aquatic organisms by birds and terrestrial animals, and (iv) harvesting of aquatic biomass by humans. Hereof, benthic macrofauna potentially affects dinitrogen emission by stimulating microbial N-cycle pathways.

Stimulation of denitrification increases the flux of nitrate from the water column into the sediment, where nitrate is reduced to dinitrogen and nitrous oxide which may then emitted to the atmosphere (Fig. 3). Thus, stimulation of denitrification potentially reduces DIN concentrations in the water column, but increases nitrous oxide emission. Stimulation of nitrification reduces the flux of ammonium and increases the flux of nitrate from the sediment into the water column. However, some of the nitrate produced by nitrification diffuses into deeper anoxic sediment layers where it is reduced to dinitrogen, which corresponds to coupled nitrification–denitrification. Thus, stimulation of nitrification potentially reduces DIN concentrations in the water column because part of the upwards diffusing ammonium is eventually converted to dinitrogen which may be emitted to the atmosphere. Stimulation of nitrification also enhances nitrous oxide emission, both directly during ammonia oxidation or nitrifier denitrification and indirectly through coupled nitrification–denitrification. Stimulation of organic matter mineralization, excretion of ammonium, and transport of ammonium across the sediment–water interface all increase the flux of ammonium from the sediment to the water column. The efflux of

ammonium can, however, not exceed the flux of PON to the benthos, but macrofauna may increase the flux of PON by biodeposition and feeding activities. Thus, stimulation of mineralization, excretion of ammonium, and transport of ammonium potentially increases DIN concentrations in the water column where it fuels primary production. The overall net effect of the stimulation of nitrogen cycling by benthic macrofauna depends on the strength of stimulation of each individual process involved in nitrogen cycling. However, these stimulation processes are in reality more complex than shown in the schematic representation of Fig. 3. The solute exchange between sediment and water is not simply mediated by one-dimensional diffusion across the sediment–water interface, but rather by diffusion and advection across the three-dimensional extension of the oxic–anoxic interface created by the activities of sediment-dwelling macrofauna (Kristensen and Kostka, 2005). Additionally, the turnover and transport of solutes undergo pronounced temporal dynamics due to periodic ventilation of the burrows and diurnal changes of macrofauna activity (Wenzhöfer and Glud, 2004).

3.2 Quantitative evaluation

3.2.1 Procedure

In the following, the results of 38 published studies are quantitatively evaluated with respect to ecosystem-level fixed nitrogen removal (Fig. 4, Table 1). The majority of studies suitable for this evaluation were conducted as laboratory experiments in which the density of a single macrofauna species was manipulated, despite the fact that benthic communities may comprise many different macrofauna species. Such use of mono-species experiments is justified when the given species occurs at extremely high density and dominates the macrofauna community. Additionally, in many of the selected studies, only a single type of animal–microbe interactions (the most popular one being "ecosystem engineering by infauna") is discussed. In reality, these studies address the net effect of several types of animal–microbe interactions that may run in parallel, both within single macrofauna species and within macrofauna communities.

Only a selected subset of data from the selected studies can be presented here, which may bias the overall outcome of this quantitative evaluation. For instance, the macrofauna density closest to the natural density, one out of several sediment types or incubation temperatures tested, and the end point of time series experiments were considered. Note also that even within a single macrofauna species, the variability of results was often substantial due to differences in animal density, sediment type, incubation length, DIN concentration, temperature, and analytical procedures used.

Figure 4 displays taxonomically grouped macrofauna species for which at least one of the following variables was determined: nitrification and denitrification rates, and ammonium and nitrate fluxes. Denitrification rates correspond to (i) the sum of rates of coupled nitrification–denitrification (D_n) and denitrification of water column nitrate (D_w) when ^{15}N-enrichment experiments were made, or to (ii) D_w alone when the acetylene inhibition technique was used. The latter is because acetylene also inhibits nitrification (i.e., $D_n = 0$) and thus the total rate of denitrification is underestimated.

3.2.2 Overview

Freshwater macrofauna is represented by the classes Insecta, Oligochaeta, and Bivalvia, while marine macrofauna is represented by the classes Crustacea, Polychaeta, and Bivalvia (Fig. 4). Freshwater insects and oligochaetes were tested at densities of 2000–38 750 individuals m^{-2}. Prominent examples occurring at such high densities in lake sediments are *Chironomus plumosus* and *Tubifex tubifex*. The presence of all insect and oligochaete species increased the areal rates of nitrification and denitrification, the ammonium efflux, and the nitrate influx. In the only two studies in which both ammonium and nitrate fluxes were measured (i.e., *C. plumosus* [93], *T. tubifex* [92]; number in [] indicates reference from which the data were taken), the animal-enhanced nitrate influx at least balanced or even exceeded the ammonium efflux.

The crustacean species tested comprise both small amphipods (e.g., *Corophium volutator*) and large decapods (e.g., *Callianassa subterranea*) and burrow in coastal marine sediments at densities of 30–19 800 individuals m^{-2}. All crustacean species in-

creased nitrification rates, in the extreme case ca. 10-fold (*Upogebia pugettensis* [18]), but only about half of them increased denitrification rates (e.g., *C. volutator*), while the other half had no significant effect on denitrification (e.g., *C. subterranea*). The presence of decapods strongly increased the ammonium efflux (e.g., *Neohelice granulata* [22]), while amphipods only had a minor effect on the ammonium flux with the exception of *Victoriopisa australiensis* [21]. Crustacean effects on nitrate fluxes were diverse, ranging from strong increases of the nitrate influx observed for *C. volutator* [90,94] and *N. granulata* [22] to increases of the nitrate efflux observed for *Trypaea australiensis* [56] and *U. pugettensis* [18]. In studies in which both ammonium and nitrate fluxes were measured, the animal-enhanced ammonium efflux often exceeded the nitrate influx, but in five studies, the presence of crustaceans increased the simultaneous efflux of ammonium and nitrate.

The bivalves are the only class for which both freshwater and marine species were tested (at densities of 440–10 000 individuals m^{-2}) for their effects on benthic nitrogen cycling. The presence of the invasive *Dreissena polymorpha* increased nitrification rates [11,67], but no other bivalve species was tested for this trait. Nearly all bivalve species increased denitrification rates, but in some cases only marginally (e.g., *Tapes philippinarum* [84]); in the presence of *Macoma balthica* [57], denitrification rates were even lower than in their absence. Ammonium effluxes were consistently enhanced by bivalves, with *T. philippinarum* [84] having the strongest effect. Nitrate fluxes were influenced in diverse ways, even within one species (i.e., *M. balthica* [41, 57, 77]), covering increases of the nitrate influx, increases of the nitrate efflux, and an inversion of the flux direction. In studies in which both ammonium and nitrate fluxes were measured, the absolute increase in ammonium efflux was always larger than any change in nitrate flux.

The marine polychaetes were tested at densities of 50–5000 individuals m^{-2}. Nitrification rates were increased in the presence of two *Nereis* species [37, 63, 81] and not tested for any other polychaete species. With one exception (i.e., *Marenzelleria viridis* [57]), all polychaete species, including *M. viridis* tested in two other studies [45,

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

64], increased denitrification rates often ca. 3-fold. Without exception, the presence of marine polychaetes increased the ammonium efflux, in some cases more than 10-fold (e.g., *Marenzelleria* sp. [45]). All polychaete species increased the nitrate influx (e.g., *Nereis* sp. [86]) or led to the inversion of a nitrate efflux to a nitrate influx (e.g., *N. virens* [41, 63, 77]). In almost all studies in which both ammonium and nitrate fluxes were measured, the absolute increase in ammonium efflux was larger than the increase in nitrate influx.

3.2.3 Essence

The general patterns of macrofauna-induced stimulation of benthic nitrogen cycling are compiled in Table 1. The two major sources of bias in this quantitative evaluation are (i) the vastly different background rates and fluxes in the sediments used for experiments and (ii) the different subsets of data provided by the individual studies (i.e., the number of observations differs between the variables). Other sources of bias have been mentioned above. Despite these biases, meaningful trends emerge due to the relatively large number of studies considered for this quantitative evaluation.

The presence of abundant benthic macrofauna species increased the areal rates of nitrification and denitrification by factors of 3.0 ± 2.3 ($n = 15$) and 2.4 ± 1.5 ($n = 39$), respectively (Tab. 1). Ammonium effluxes and nitrate influxes were enhanced by factors of 5.3 ± 4.1 ($n = 26$) and 2.2 ± 2.2 ($n = 14$), respectively. Thus, while both nitrification and denitrification were stimulated to approximately the same degree, the stimulation of the ammonium efflux was considerably higher than the stimulation of the nitrate influx. The most likely explanation for this observation is that due to the animal-enhanced solute transport, ammonium crosses the nitrification layer which in diffusive settings acts as an efficient barrier for ammonium (Stief et al., 2002). Stimulation factors may not be representative measures of the eventual changes in DIN concentrations in the water column when background rates and fluxes differ largely (see above). Therefore, it is necessary to also look at the absolute changes in ammonium and nitrate fluxes imposed on sediments by benthic macrofauna (Table 1). On average, the ammonium

efflux was enhanced by $235 \pm 285\,\mu\mathrm{mol\,N\,m^{-2}\,h^{-1}}$ ($n = 31$), while the nitrate influx was only enhanced by $118 \pm 381\,\mu\mathrm{mol\,N\,m^{-2}\,h^{-1}}$ ($n = 28$). Thus, the removal of fixed nitrogen as nitrate (via animal-enhanced denitrification) is more than offset by the increase in fixed nitrogen as ammonium (via animal-enhanced solute transport). Against this background, it is not surprising that the DIN efflux from the sediments used in the 38 studies increased on average from 24 to $162\,\mu\mathrm{mol\,N\,m^{-2}\,h^{-1}}$ ($n = 27$) when benthic macrofauna was present.

4 Nitrous oxide emission associated with benthic macrofauna

Fixed nitrogen removal due to macrofauna activities is not only counteracted by the enhanced ammonium efflux from the sediment into the water column, but also by enhanced nitrous oxide emission. This phenomenon has first been noted for the ubiquitous and highly abundant freshwater midge larva *C. plumosus* (Svensson, 1998) and thereafter for many other freshwater and marine macrofauna species (Stief et al., 2009; Heisterkamp et al., 2010). Svensson (1998) ascribed the emission of nitrous oxide from lake sediment colonized by *C. plumosus* to nitrification activity inside the larval burrows. Stief and coworkers (2009) discovered nitrous oxide production due to denitrification activity inside the gut of *C. plumosus* larvae and other filter- and deposit-feeding freshwater macrofauna. Heisterkamp and coworkers (2010) additionally found nitrous oxide production occurring in the biofilm covering the shell of a marine snail. Thus, nitrous oxide production can be (i) indirectly associated with benthic macrofauna and mediated by microorganisms in their immediate microenvironment (e.g., their burrow) and/or (ii) directly associated with benthic macrofauna and mediated by microorganisms in their guts or their shell biofilms. The first case fits into the category ecosystem engineering, while the second case fits into the categories grazing and symbiosis.

Emission of nitrous oxide produced in the burrows and guts of *C. plumosus* larvae and other sediment-dwelling macrofauna is greatly facilitated by burrow ventilation. At a density of 745 individuals $\mathrm{m^{-2}}$, for instance, *C. plumosus* transports $1300\,\mathrm{L\,m^{-2}\,d^{-1}}$

lake water through the sediment by burrow ventilation (Roskosch et al., 2010). Thereby, the larvae simultaneously enhance the nitrate influx into the sediment (potentially stimulating denitrification in burrows and guts) and the ammonium and nitrous oxide effluxes from the sediment. Approximately 15–30% of the increased nitrous oxide emission is due to gut denitrification, while the remainder is due to stimulated nitrification and denitrification in *C. plumosus* burrows (Svensson, 1998; Stief et al., 2009). The nitrous oxide yield of gut denitrification (i.e., the $N_2O/N_2 + N_2O$ emission ratio) is 43–68% and thus significantly higher than the 0.1–0.5% reported for aquatic sediments (Seitzinger and Kroeze, 1998; Stief et al., 2009, 2010). The high nitrous oxide yields are explained by incomplete induction of the denitrification sequence or by partial inhibition of the nitrous oxide reduction step by low oxygen concentrations. At a density of 3450 individuals m^{-2}, *C. plumosus* larvae increase the nitrous oxide yield of sediment-water gas fluxes ca. 2.5-fold (Stief et al., 2009). Aside from *C. plumosus*, only two more sediment-dwelling freshwater species have been studied, the mayfly *Ephemera danica* and the alderfly *Sialis lutaris* (Stief and Schramm, 2010). *C. plumosus* and *E. danica* larvae contribute to the total N_2O efflux by gut denitrification and by stimulating sedimentary denitrification, while *S. lutaria* only stimulates sedimentary denitrification.

A recent study revealed that the invasive bivalve *D. polymorpha* potentially increases the nitrous oxide efflux 400–3000-fold at natural densities of 100 000–700 000 individuals m^{-2} (Svenningsen et al., 2012). One third of the nitrous oxide emitted by *D. polymorpha* is produced in the shell biofilm as a by-product of ammonia-oxidation; the remaining two thirds are produced in the gut as an intermediate of denitrification. The high rate of ammonium excretion by *D. polymorpha* (Conroy et al., 2005) thus not only fuels coupled nitrification–denitrification in the sediment (Bruesewitz et al., 2008), but also the nitrous-oxide-producing bacteria in the biofilm on their own shell. Meanwhile, also marine mollusks were found to emit nitrous oxide produced in their shell biofilm by both nitrification and denitrification (Heisterkamp et al., 2013). Ammonium excretion rates of the animal hosts were by far higher than the rates of nitrous oxide emission from the shell biofilms, meaning that nitrous oxide production may be

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◂◂ | ▸▸

◂ | ▸

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

uncoupled from ambient DIN supply. Additionally, the nutrient-rich microenvironment shapes specific microbial communities, since nitrous oxide emission rates from living animals with shell biofilms are higher than from stones or shell debris collected nearby (Heisterkamp et al., 2013).

Nitrification activity is also directly associated with the marine bivalve *Mytilus galloprovincialis* that is extensively used for suspended mussel farming (Welsh and Castadelli, 2004). It has been speculated that nitrogen cycling in the mussel rope community rivals nitrogen cycling in sediments underlying the mussel farms (Nizzoli et al., 2005). Future studies should investigate whether and how much nitrous oxide is emitted by *M. galloprovincialis* and other extensively cultivated mussels and clams. The same is true for oyster reefs and mussel banks that are restored with the aim to improve water quality (Plutchak et al., 2010; Stadmark and Conley, 2011; Rose et al., 2012; Carmichael et al., 2012; Kellogg et al., 2013), but may in fact be significant sources of nitrous oxide. Further, animals kept in aquaculture facilities at very high nutrient concentrations should be investigated for their potential to emit nitrous oxide, since first experiments revealed extremely high rates of nitrous oxide production directly associated with the widely used shrimp *Litopenaeus vannamei* (Heisterkamp et al., 2010).

References

Aller, R. C. and Aller, J. Y.: The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments, J. Mar. Res., 56, 905–936, 1998.

Altmann, D., Stief, P., Amann, R., and de Beer, D.: Nitrification in freshwater sediments as influenced by insect larvae: quantification by microsensors and fluorescence in situ hybridization, Microb. Ecol., 48, 145–153, 2004.

Autio, L., Makela, K., Lehtonen, K. K., Kuparinen, J., and Haahti, H.: Effects of algal sedimentation and *Monoporeia affinis* on nutrient fluxes, pore water profiles and denitrification in sediment microcosms, Boreal Environ. Res., 8, 229–243, 2003.

Banks, J. L., Ross, D. J., Keough, M. J., Macleod, C. K., Keane, J., and Eyre, B. D.: Influence of a burrowing, metal-tolerant polychaete on benthic metabolism, denitrification and nitrogen regeneration in contaminated estuarine sediments, Mar. Pollut. Bull., 68, 30–37, 2013.

Bartoli, M., Nizzoli, D., Welsh, D. T., and Viaroli, P.: Short-term influence of recolonisation by the polychaete worm *Nereis succinea* on oxygen and nitrogen fluxes and denitrification: a microcosm study, Hydrobiologia, 431, 165–174, 2000.

Bayer, C., Heindl, N. R., Rinke, C., Lucker, S., Ott, J. A., and Bulgheresi, S.: Molecular characterization of the symbionts associated with marine nematodes of the genus *Robbea*, Environ. Microbiol. Reports, 1, 136–144, 2009.

Bayer, K., Schmitt, S., and Hentschel, U.: Physiology, phylogeny and in situ evidence for bacterial and archaeal nitrifiers in the marine sponge *Aplysina aerophoba*, Environ. Microbiol., 10, 2942–2955, 2008.

Bertics, V. J., Sohm, J. A., Magnabosco, C., and Ziebis, W.: Denitrification and nitrogen fixation dynamics in the area surrounding an individual ghost shrimp (*Neotrypaea californiensis*) burrow system, Appl. Environ. Microb., 78, 3864–3872, 2012.

Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J. J., Soetaert, K., Vincx, M., and Vanaverbeke, J.: Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation, Mar. Ecol.-Prog. Ser., 399, 173–186, 2010.

Bruesewitz, D. A., Tank, J. L., Bernot, M. J., Richardson, W. B., and Strauss, E. A.: Seasonal effects of the zebra mussel (*Dreissena polymorpha*) on sediment denitrification rates in Pool 8 of the Upper Mississippi River, Can. J. Fish. Aquat. Sci., 63, 957–969, 2006.

Bruesewitz, D. A., Tank, J. L., and Bernot, M. J.: Delineating the effects of zebra mussels (*Dreissena polymorpha*) on N transformation rates using laboratory mesocosms, J. N. Am. Benthol. Soc., 27, 236–251, 2008.

Bruesewitz, D. A., Tank, J. L., and Hamilton, S. K.: Seasonal effects of zebra mussels on littoral nitrogen transformation rates in Gull Lake, Michigan, USA, Freshwater Biol., 54, 1427–1443, 2009.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Title Page

Abstract	Introduction
Conclusions	References
Tables	Figures

◄◄   ►►

◄   ►

Back   Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Carlsson, M. S., Glud, R. N., and Petersen, J. K.: Degradation of mussel (*Mytilus edulis*) fecal pellets released from hanging long-lines upon sinking and after settling at the sediment, Can. J. Fish. Aquat. Sci., 67, 1376–1387, 2010.

Carmichael, R. H., Walton, W., and Clark, H.: Bivalve-enhanced nitrogen removal from coastal estuaries, Can. J. Fish. Aquat. Sci., 69, 1131–1149, 2012.

Christensen, B., Vedel, A., and Kristensen, E.: Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes, Mar. Ecol.-Prog. Ser., 192, 203–217, 2000.

Conroy, J. D., Edwards, W. J., Pontius, R. A., Kane, D. D., Zhang, H. Y., Shea, J. F., Richey, J. N., and Culver, D. A.: Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie, Freshwater Biol., 50, 1146–1162, 2005.

Dame, R. F., Spurrier, J. D., and Zingmark, R. G.: In situ metabolism of an oyster reef, J. Exp. Mar. Biol. Ecol., 164, 147–159, 1992.

D'Andrea, A. F. and DeWitt, T. H.: Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: density-dependent effects on organic matter remineralization and nutrient cycling, Limnol. Oceanogr., 54, 1911–1932, 2009.

Deines, P., Bodelier, P. L. E., and Eller, G.: Methane-derived carbon flows through methane-oxidizing bacteria to higher trophic levels in aquatic systems, Environ. Microbiol., 9, 1126–1134, 2007.

Dollhopf, S. L., Hyun, J. H., Smith, A. C., Adams, H. J., O'Brien, S., and Kostka, J. E.: Quantification of ammonia-oxidizing bacteria and factors controlling nitrification in salt marsh sediments, Appl. Environ. Microb., 71, 240–246, 2005.

Dunn, R. J. K., Welsh, D. T., Jordan, M. A., Teasdale, P. R., and Lemckert, C. J.: Influence of natural amphipod (*Victoriopisa australiensis*) (Chilton, 1923) population densities on benthic metabolism, nutrient fluxes, denitrification and DNRA in sub-tropical estuarine sediment, Hydrobiologia, 628, 95–109, 2009.

Fanjul, E., Bazterrica, M. C., Escapa, M., Grela, M. A., and Iribarne, O.: Impact of crab bioturbation on benthic flux and nitrogen dynamics of Southwest Atlantic intertidal marshes and mudflats, Estuar. Coast. Shelf S., 92, 629–638, 2011.

Feuchtmayr, H., Moran, R., Hatton, K., Connor, L., Heyes, T., Moss, B., Harvey, I., and Atkinson, D.: Global warming and eutrophication: effects on water chemistry and autotrophic com-

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

⏮ | ⏭

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

munities in experimental hypertrophic shallow lake mesocosms, J. Appl. Ecol., 46, 713–723, 2009.

Fiore, C. L., Jarett, J. K., Olson, N. D., and Lesser, M. P.: Nitrogen fixation and nitrogen transformations in marine symbioses, Trends Microbiol., 18, 455–463, 2010.

Fiore, C. L., Labrie, M., and Lesser, M. P.: Pumping activity and nitrogen cycling in the giant barrel sponge, *Xestospongia muta*, Integr. Comp. Biol., 52, Abstract E245, 2012.

Fonseca Leal, J. J., Esteves, F. D., Farjalla, V. F., and Enrich-Prast, A.: Effect of *Campsurus notatus* on NH_4^+, DOC fluxes, O_2 uptake and bacterioplankton production in experimental microcosms with sediment–water interface of an Amazonian lake impacted by bauxite tailings, Int. Rev. Hydrobiol., 88, 167–178, 2003.

Gardner, W. S., Nalepa, T. F., Slavens, D. R., and Laird, G. A.: Patterns and rates of nitrogen release by benthic Chironomidae and Oligochaeta, Can. J. Fish. Aquat. Sci., 40, 259–266, 1983.

Gardner, W. S., Cavaletto, J. F., Johengen, T. H., Johnson, J. R., Heath, R. T., and Cotner, J. B.: Effects of the zebra mussel, *Dreissena polymorpha*, on community nitrogen dynamics in Saginaw Bay, Lake Huron, J. Great Lakes Res., 21, 529–544, 1995.

Gardner, W. S., Yang, L. Y., Cotner, J. B., Johengen, T. H., and Lavrentyev, P. J.: Nitrogen dynamics in sandy freshwater sediments (Saginaw Bay, Lake Huron), J. Great Lakes Res., 27, 84–97, 2001.

Gilbert, F., Souchu, P., Bianchi, M., and Bonin, P.: Influence of shellfish farming activities on nitrification, nitrate reduction to ammonium and denitrification at the water–sediment interface of the Thau lagoon, France, Mar. Ecol.-Prog. Ser., 151, 143–153, 1997.

Gilbertson, W. W., Solan, M., and Prosser, J. I.: Differential effects of microorganism-invertebrate interactions on benthic nitrogen cycling, FEMS Microbiol. Ecol., 82, 11–22, 2012.

Girguis, P. R., Lee, R. W., Desaulniers, N., Childress, J. J., Pospesel, M., Felbeck, H., and Zal, F.: Fate of nitrate acquired by the tubeworm *Riftia pachyptila*, Appl. Environ. Microb., 66, 2783–2790, 2000.

Goedkoop, W. and Johnson, R. K.: Exploitation of sediment bacterial carbon by juveniles of the amphipod *Monoporeia affinis*, Freshwater Biol., 32, 553–563, 1994.

Gruber, N. and Galloway, J. N.: An Earth-system perspective of the global nitrogen cycle, Nature, 451, 293–296, 2008.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Gutierrez, J. L., Jones, C. G., Strayer, D. L., and Iribarne, O. O.: Mollusks as ecosystem engineers: the role of shell production in aquatic habitats, Oikos, 101, 79–90, 2003.

Hamilton, D. J., Ankney, C. D., and Bailey, R. C.: Predation of zebra mussels by diving ducks – an exclosure study, Ecology, 75, 521–531, 1994.

5   Hansen, K. and Kristensen, E.: The impact of the polychaete *Nereis diversicolor* and enrichment with macroalgal (*Chaetomorpha linum*) detritus on benthic metabolism and nutrient dynamics in organic-poor and organic-rich sediment, J. Exp. Mar. Biol. Ecol., 231, 201–223, 1998.

Hatcher, A., Grant, J., and Schofield, B.: Effects of suspended mussel culture (*Mytilus* spp.)
10   on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay, Mar. Ecol.-Prog. Ser., 115, 219–235, 1994.

Heisterkamp, I. M., Schramm, A., de Beer, D., and Stief, P.: Nitrous oxide production associated with coastal marine invertebrates, Mar. Ecol.-Prog. Ser., 415, 1–9, 2010.

Heisterkamp, I. M., Schramm, A., Larsen, L. H., Svenningsen, N. B., Lavik, G., de Beer, D., and
15   Stief, P.: Shell-biofilm-associated nitrous oxide production in marine molluscs: processes, precursors, and relative importance, Environ. Microbiol., 15, 1943–1955, 2013.

Henriksen, K., Rasmussen, M. B., and Jensen, A.: Effect of bioturbation on microbial nitrogen transformations in the sediment and fluxes of ammonium and nitrate to the overlying water, Ecol. Bull., 35, 193–205, 1983.

20   Hentschel, U. and Felbeck, H.: Nitrate respiration in the hydrothermal vent tubeworm *Riftia pachyptila*, Nature, 366, 338–340, 1993.

Hentschel, U., Berger, E. C., Bright, M., Felbeck, H., and Ott, J. A.: Metabolism of nitrogen and sulfur in ectosymbiotic bacteria of marine nematodes (Nematoda, Stilbonematinae), Mar. Ecol.-Prog. Ser., 183, 149–158, 1999.

25   Hentschel, U., Usher, K. M., and Taylor, M. W.: Marine sponges as microbial fermenters, FEMS Microbiol. Ecol., 55, 167–177, 2006.

Hietanen, S., Laine, A. O., and Lukkari, K.: The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics, J. Exp. Mar. Biol. Ecol., 352, 89–102, 2007.

Higgins, C. B., Stephenson, K., and Brown, B. L.: Nutrient bioassimilation capacity of aquacul-
30   tured oysters: quantification of an ecosystem service, J. Environ. Qual., 40, 271–277, 2011.

Higgins, C. B., Tobias, C., Piehler, M. F., Smyth, A. R., Dame, R. F., Stephenson, K., and Brown, B. L.: Effect of aquacultured oyster biodeposition on sediment N_2 production in Chesapeake Bay, Mar. Ecol.-Prog. Ser., 473, 7–27, 2013.

Higgins, S. N. and Vander Zanden, M. J.: What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems, Ecol. Monogr., 80, 179–196, 2010.

Hoffmann, F., Roy, H., Bayer, K., Hentschel, U., Pfannkuchen, M., Bruemmer, F., and de Beer, D.: Oxygen dynamics and transport in the Mediterranean sponge *Aplysina aerophoba*, Mar. Biol., 153, 1257–1264, 2008.

Hoffmann, F., Radax, R., Woebken, D., Holtappels, M., Lavik, G., Rapp, H. T., Schläppy, M. L., Schleper, C., and Kuypers, M. M. M.: Complex nitrogen cycling in the sponge *Geodia barretti*, Environ. Microbiol., 11, 2228–2243, 2009.

Howarth, R., Chan, F., Conley, D. J., Garnier, J., Doney, S. C., Marino, R., and Billen, G.: Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems, Front. Ecol. Environ., 9, 18–26, 2011.

Howe, R. L., Rees, A. P., and Widdicombe, S.: The impact of two species of bioturbating shrimp (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification, J. Mar. Biol. Assoc. UK, 84, 629–632, 2004.

Jimenez, E. and Ribes, M.: Sponges as a source of dissolved inorganic nitrogen: nitrification mediated by temperate sponges, Limnol. Oceanogr., 52, 948–958, 2007.

Johnson, R. K., Boström, B., and Van de Bund, W. J.: Interactions between *Chironomus plumosus* L., and the microbial community in surficial sediments of a shallow eutrophic lake, Limnol. Oceanogr., 34, 992–1003, 1989.

Jones, C. G., Lawton, J. H., and Shachak, M.: Organisms as ecosystem engineers, Oikos, 69, 373–386, 1994.

Jordan, M. A., Welsh, D. T., Dunn, R. J. K., and Teasdale, P. R.: Influence of *Trypaea australiensis* population density on benthic metabolism and nitrogen dynamics in sandy estuarine sediment: a mesocosm simulation, J. Sea Res., 61, 144–152, 2009.

Karlson, K., Hulth, S., Ringdahl, K., and Rosenberg, R.: Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling, Mar. Ecol.-Prog. Ser., 294, 35–49, 2005.

Karlson, K., Hulth, S., and Rosenberg, R.: Density of *Monoporeia affinis* and biogeochemistry in Baltic Sea sediments, J. Exp. Mar. Biol. Ecol., 344, 123–135, 2007.

Kellogg, M. L., Cornwell, J. C., Owens, M. S., and Paynter, K. T.: Denitrification and nutrient assimilation on a restored oyster reef, Mar. Ecol.-Prog. Ser., 480, 1–19, 2013.

Kemp, P. F.: Potential impact on bacteria of grazing by a macrofaunal deposit-feeder, and the fate of bacterial production, Mar. Ecol.-Prog. Ser., 36, 151–161, 1987.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

|◀ | ▶|

◀ | ▶

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Kikuchi, Y., Bomar, L., and Graf, J.: Stratified bacterial community in the bladder of the medicinal leech, *Hirudo verbena*, Environ. Microbiol., 11, 2758–2770, 2009.

Kristensen, E. and Kostka, J. E.: Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions, in: Interactions Between Macro- and Microorganisms in Marine Sediments, edited by: Kristensen, E., Haese, R. R., and Kostka, J. E., AGU, Washington, DC, 125–157, 2005.

Kristensen, E., Jensen, M. H., and Aller, R. C.: Direct measurement of dissolved inorganic nitrogen exchange and denitrification in individual polychaete *Nereis virens* burrows, J. Mar. Res., 49, 355–378, 1991.

Kristensen, E., Hansen, T., Delefosse, M., Banta, G. T., and Quintana, C. O.: Contrasting effects of the polychaetes *Marenzelleria viridis* and *Nereis diversicolor* on benthic metabolism and solute transport in sandy coastal sediment, Mar. Ecol.-Prog. Ser., 425, 125–139, 2011.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O., and Banta, G. T.: What is bioturbation?, The need for a precise definition for fauna in aquatic sciences, Mar. Ecol.-Prog. Ser., 446, 285–302, 2012.

Laverock, B., Gilbert, J. A., Tait, K., Osborn, A. M., and Widdicombe, S.: Bioturbation: impact on the marine nitrogen cycle, Biochem. Soc. T., 39, 315–320, 2011.

Lavrentyev, P. J., Gardner, W. S., and Yang, L.: Effects of the zebra mussel on nitrogen dynamics and the microbial community at the sediment–water interface, Aquat. Microb. Ecol., 21, 187–194, 2000.

Lechene, C. P., Luyten, Y., McMahon, G., and Distel, D. L.: Quantitative imaging of nitrogen fixation by individual bacteria within animal cells, Science, 317, 1563–1566, 2007.

Lenihan, H. S.: Physical-biological coupling on oyster reefs: how habitat structure influences individual performance, Ecol. Monogr., 69, 251–275, 1999.

Levin, L. A. and Michener, R. H.: Isotopic evidence for chemosynthesis-based nutrition of macrobenthos: the lightness of being at Pacific methane seeps, Limnol. Oceanogr., 47, 1336–1345, 2002.

Lewandowski, J., Laskov, C., and Hupfer, M.: The relationship between *Chironomus plumosus* burrows and the spatial distribution of pore-water phosphate, iron and ammonium in lake sediments, Freshwater Biol., 52, 331–343, 2007.

Markert, A., Wehrmann, A., and Kroncke, I.: Recently established *Crassostrea*-reefs versus native *Mytilus*-beds: differences in ecosystem engineering affects the macrofaunal commu-

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

nities (Wadden Sea of Lower Saxony, southern German Bight), Biol. Invasions, 12, 15–32, 2010.

Martinez-Garcia, M., Stief, P., Diaz-Valdes, M., Wanner, G., Ramos-Espla, A., Dubilier, N., and Anton, J.: Ammonia-oxidizing Crenarchaeota and nitrification inside the tissue of a colonial ascidian, Environ. Microbiol., 10, 2991–3001, 2008.

Mayer, M. S., Schaffner, L., and Kemp, W. M.: Nitrification potentials of benthic macrofaunal tubes and burrow walls: effects of sediment NH_4^+ and animal irrigation behavior, Mar. Ecol.-Prog. Ser., 121, 157–169, 1995.

McFall-Ngai, M., Hadfield, M. G., Bosch, T. C. G., Carey, H. V., Domazet-Loso, T., Douglas, A. E., Dubilier, N., Eberl, G., Fukami, T., Gilbert, S. F., Hentschel, U., King, N., Kjelleberg, S., Knoll, A. H., Kremer, N., Mazmanian, S. K., Metcalf, J. L., Nealson, K., Pierce, N. E., Rawls, J. F., Reid, A., Ruby, E. G., Rumpho, M., Sanders, J. G., Tautz, D., and Wernegreen, J. J.: Animals in a bacterial world, a new imperative for the life sciences, P. Natl. Acad. Sci., 110, 3229–3236, 2013.

Meysman, F. J. R., Middelburg, J. J., and Heip, C. H. R.: Bioturbation: a fresh look at Darwin's last idea, Trends Ecol. Evol., 21, 688–695, 2006.

Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B., and Stora, G.: The functional group approach to bioturbation: II. the effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment–water interface, J. Exp. Mar. Biol. Ecol., 337, 178–189, 2006.

Na, T., Gribsholt, B., Galaktionov, O. S., Lee, T., and Meysman, F. J. R.: Influence of advective bio-irrigation on carbon and nitrogen cycling in sandy sediments, J. Mar. Res., 66, 691–722, 2008.

Newell, R. I. E., Cornwell, J. C., and Owens, M. S.: Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study, Limnol. Oceanogr., 47, 1367–1379, 2002.

Newell, R. I. E., Fisher, T. R., Holyoke, R. R., and Cornwell, J. C.: Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA, comparative roles of suspension-feeders, Ecosystems, 47, 93–120, 2005.

Nielsen, O. I., Gribsholt, B., Kristensen, E., and Revsbech, N. P.: Microscale distribution of oxygen and nitrate in sediment inhabited by *Nereis diversicolor*: spatial patterns and estimated reaction rates, Aquat. Microb. Ecol., 34, 23–32, 2004.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Nixon, S. W.: Coastal marine eutrophication: a definition, social causes, and future concerns, Ophelia, 41, 199–219, 1995.

Nizzoli, D., Welsh, D. T., Bartoli, M., and Viaroli, P.: Impacts of mussel (*Mytilus galloprovincialis*) farming on oxygen consumption and nutrient recycling in a eutrophic coastal lagoon, Hydrobiologia, 550, 183–198, 2005.

Nizzoli, D., Bartoli, M., and Viaroli, P.: Nitrogen and phosphorous budgets during a farming cycle of the Manila clam *Ruditapes philippinarum*: an in situ experiment, Aquaculture, 261, 98–108, 2006a.

Nizzoli, D., Welsh, D. T., Fano, E. A., and Viaroli, P.: Impact of clam and mussel farming on benthic metabolism and nitrogen cycling, with emphasis on nitrate reduction pathways, Mar. Ecol.-Prog. Ser., 315, 151–165, 2006b.

Nizzoli, D., Bartoli, M., Cooper, M., Welsh, D. T., Underwood, G. J. C., and Viaroli, P.: Implications for oxygen, nutrient fluxes and denitrification rates during the early stage of sediment colonisation by the polychaete *Nereis* spp. in four estuaries, Estuar. Coast. Shelf S., 75, 125–134, 2007.

Papaspyrou, S., Gregersen, T., Cox, R. P., Thessalou-Legaki, M., and Kristensen, E.: Sediment properties and bacterial community in burrows of the ghost shrimp *Pestarella tyrrhena* (Decapoda: Thalassinidea), Aquat. Microb. Ecol., 38, 181–190, 2005.

Pascal, P. Y., Dupuy, C., Mallet, C., Richard, P., and Niquil, N.: Bacterivory by benthic organisms in sediment: quantification using ^{15}N-enriched bacteria, J. Exp. Mar. Biol. Ecol., 355, 18–26, 2008.

Pejchar, L. and Mooney, H. A.: Invasive species, ecosystem services and human well-being, Trends Ecol. Evol., 24, 497–504, 2009.

Pelegri, S. P. and Blackburn, T. H.: Bioturbation effects of the amphipod *Corophium volutator* on microbial nitrogen transformations in marine sediments, Mar. Biol., 121, 253–258, 1994.

Pelegri, S. P. and Blackburn, T. H.: Effect of bioturbation by *Nereis* sp., *Mya arenaria* and *Cerastoderma* sp. on nitrification and denitrification in estuarine sediments, Ophelia, 42, 289–299, 1995a.

Pelegri, S. P. and Blackburn, T. H.: Effects of *Tubifex tubifex* (Oligochaeta: Tubificidae) on N-mineralization in freshwater sediments, measured with ^{15}N isotopes, Aquat. Microb. Ecol., 9, 289–294, 1995b.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Pelegri, S. P. and Blackburn, T. H.: Nitrogen cycling in lake sediments bioturbated by *Chironomus plumosus* larvae, under different degrees of oxygenation, Hydrobiologia, 325, 231–238, 1996.

Pelegri, S. P., Nielsen, L. P., and Blackburn, T. H.: Denitrification in estuarine sediment stimulated by the irrigation activity of the amphipod *Corophium volutator*, Mar. Ecol.-Prog. Ser., 105, 285–290, 1994.

Piehler, M. F. and Smyth, A. R.: Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services, Ecosphere, 2, 1–16, 2011.

Plante, C. J. and Jumars, P.: The microbial environment of marine deposit-feeder guts characterized via microelectrodes, Microb. Ecol., 23, 257–277, 1992.

Plante, C. J. and Mayer, L. M.: Distribution and efficiency of bacteriolysis in the gut of *Arenicola marina* and three additional deposit feeders, Mar. Ecol.-Prog. Ser., 109, 183–194, 1994.

Plante, C. J. and Wilde, S. B.: Bacterial recolonization of deposit-feeder egesta: in situ regrowth or immigration?, Limnol. Oceanogr., 46, 1171–1181, 2001.

Plutchak, R., Major, K., Cebrian, J., Foster, C. D., Miller, M. E. C., Anton, A., Sheehan, K. L., Heck, K. L., and Powers, S. P.: Impacts of oyster reef restoration on primary productivity and nutrient dynamics in tidal creeks of the North Central Gulf of Mexico, Estuar. Coast., 33, 1355–1364, 2010.

Poulsen, M., Kofoed, M. V. W., Larsen, L. H., Schramm, A., and Stief, P.: *Chironomus plumosus* larvae increase fluxes of denitrification products and diversity of nitrate-reducing bacteria in freshwater sediment, Syst. Appl. Microbiol., 2013.

Prins, T. C. and Smaal, A. C.: The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde Estuary (the Netherlands), Hydrobiologia, 283, 413–429, 1994.

Rabalais, N. N.: Nitrogen in aquatic ecosystems, Ambio, 31, 102–112, 2002.

Radax, R., Hoffmann, F., Rapp, H. T., Leininger, S., and Schleper, C.: Ammonia-oxidizing archaea as main drivers of nitrification in cold-water sponges, Environ. Microbiol., 14, 909–923, 2012a.

Radax, R., Rattei, T., Lanzen, A., Bayer, C., Rapp, H. T., Urich, T., and Schleper, C.: Metatranscriptomics of the marine sponge *Geodia barretti*: tackling phylogeny and function of its microbial community, Environ. Microbiol., 14, 1308–1324, 2012b.

Rose, J. M., Ferreira, J. G., Stephenson, K., Bricker, S. B., Tedesco, M., and Wikfors, G. H.: Comment on Stadmark and Conley (2011) "Mussel farming as a nutrient reduction measure

in the Baltic Sea: Consideration of nutrient biogeochemical cycles", Mar. Pollut. Bull., 64, 449–451, 2012.

Roskosch, A., Morad, M. R., Khalili, A., and Lewandowski, J.: Bioirrigation by *Chironomus plumosus*: advective flow investigated by particle image velocimetry, J. N. Am. Benthol. Soc., 29, 789–802, 2010.

Satoh, H., Nakamura, Y., and Okabe, S.: Influences of infaunal burrows on the community structure and activity of ammonia-oxidizing bacteria in intertidal sediments, Appl. Environ. Microb., 73, 1341–1348, 2007.

Schläppy, M. L., Hoffmann, F., Roy, H., Wijffels, R. H., Mendola, D., Sidri, M., and de Beer, D.: Oxygen dynamics and flow patterns of *Dysidea avara* (Porifera: Demospongiae), J. Mar. Biol. Assoc. UK, 87, 1677–1682, 2007.

Schläppy, M. L., Schottner, S. I., Lavik, G., Kuypers, M. M. M., de Beer, D., and Hoffmann, F.: Evidence of nitrification and denitrification in high and low microbial abundance sponges, Mar. Biol., 157, 593–602, 2010a.

Schläppy, M. L., Weber, M., Mendola, D., Hoffmann, F., and de Beer, D.: Heterogeneous oxygenation resulting from active and passive flow in two Mediterranean sponges, *Dysidea avara* and *Chondrosia reniformis*, Limnol. Oceanogr., 55, 1289–1300, 2010b.

Seitzinger, S. P. and Kroeze, C.: Global distribution of nitrous oxide production and N inputs in freshwater and coastal marine ecosystems, Global Biogeochem. Cy., 12, 93–113, 1998.

Souchu, P., Vaquer, A., Collos, Y., Landrein, S., Deslous-Paoli, J.-M., and Bibent, B.: Influence of shellfish farming activities on the biogeochemical composition of the water column in Thau lagoon, Mar. Ecol.-Prog. Ser., 218, 141–152, 2001.

Stadmark, J. and Conley, D. J.: Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles, Mar. Pollut. Bull., 62, 1385–1388, 2011.

Stenton-Dozey, J., Probyn, T., and Busby, A.: Impact of mussel (*Mytilus galloprovincialis*) raft-culture on benthic macrofauna, in situ oxygen uptake, and nutrient fluxes in Saldanha Bay, South Africa, Can. J. Fish. Aquat. Sci., 58, 1021–1031, 2001.

Stief, P.: Enhanced exoenzyme activities in sediments in the presence of deposit-feeding *Chironomus riparius* larvae, Freshwater Biol., 52, 1807–1819, 2007.

Stief, P. and de Beer, D.: Probing the microenvironment of freshwater sediment macrofauna: implications of deposit-feeding and bioirrigation for nitrogen cycling, Limnol. Oceanogr., 51, 2538–2548, 2006.

Stief, P. and Eller, G.: The gut microenvironment of sediment-dwelling *Chironomus plumosus* larvae as characterised with O_2, pH and redox microsensors, J. Comp. Physiol. B, 176, 673–683, 2006.

Stief, P. and Hölker, F.: Trait-mediated indirect effects of predatory fish on microbial mineralization in aquatic sediments, Ecology, 87, 3152–3159, 2006.

Stief, P. and Schramm, A.: Regulation of nitrous oxide emission associated with benthic invertebrates, Freshwater Biol., 55, 1647–1657, 2010.

Stief, P., de Beer, D., and Neumann, D.: Small scale distribution of nitrite in freshwater microcosms: the role of nitrate and oxygen availability, and sediment permeability, Microb. Ecol., 43, 367–378, 2002.

Stief, P., Altmann, D., de Beer, D., Bieg, R., and Kureck, A.: Microbial activities in the burrow environment of the potamal mayfly *Ephoron virgo*, Freshwater Biol., 49, 1152–1163, 2004.

Stief, P., Poulsen, M., Nielsen, L. P., Brix, H., and Schramm, A.: Nitrous oxide emission by aquatic macrofauna, P. Natl. Acad. Sci., 106, 4296–4300, 2009.

Stief, P., Polerecky, L., Poulsen, M., and Schramm, A.: Control of nitrous oxide emission from *Chironomus plumosus* larvae by nitrate and temperature, Limnol. Oceanogr., 55, 872–884, 2010.

Strayer, D. L.: Twenty years of zebra mussels: lessons from the mollusk that made headlines, Front. Ecol. Environ., 7, 135–141, 2009.

Svenningsen, N. B., Heisterkamp, I. M., Sigby-Clausen, M., Larsen, L. H., Nielsen, L. P., Stief, P., and Schramm, A.: Shell biofilm nitrification and gut denitrification contribute to emission of nitrous oxide by the invasive freshwater mussel *Dreissena polymorpha* (zebra mussel), Appl. Environ. Microb., 78, 4505–4509, 2012.

Svensson, J. M.: Influence of *Chironomus plumosus* larvae on ammonium flux and denitrification (measured by the acetylene blockage- and the isotope pairing-technique) in eutrophic lake sediment, Hydrobiologia, 346, 157–168, 1997.

Svensson, J. M.: Emission of N_2O, nitrification and denitrification in a eutrophic lake sediment bioturbated by *Chironomus plumosus*, Aquat. Microb. Ecol., 14, 289–299, 1998.

Svensson, J. M. and Leonardson, L.: Effects of bioturbation by tube-dwelling chironomid larvae on oxygen uptake and denitrification in eutrophic lake sediments, Freshwater Biol., 35, 289–300, 1996.

Svensson, J. M., Enrich-Prast, A., and Leonardson, L.: Nitrification and denitrification in a eutrophic lake sediment bioturbated by oligochaetes, Aquat. Microb. Ecol., 23, 177–186, 2001.

Stimulation of microbial nitrogen cycling in aquatic ecosystems

P. Stief

Tang, K. W., Glud, R. N., Glud, A., Rysgaard, S., and Nielsen, T. G.: Copepod guts as biogeochemical hotspots in the sea: evidence from microelectrode profiling of *Calanus* spp., Limnol. Oceanogr., 56, 666–672, 2011.

Thamdrup, B.: New pathways and processes in the global nitrogen cycle, Annu. Rev. Ecol. Evol. S., 43, 407–428, 2012.

Thamdrup, B. and Dalsgaard, T.: Nitrogen cycling in sediments, in: Microbial Ecology of the Oceans., edited by: Kirchman, D. L., John Wiley and Sons, New York, 527–568, 2008.

Van de Bund, W. J., Goedkoop, W., and Johnson, R. K.: Effects of deposit-feeder activity on bacterial production and abundance in profundal lake sediment, J. N. Am. Benthol. Soc., 13, 532–539, 1994.

Wahl, M., Goecke, F., Labes, A., Dobretsov, S., and Weinberger, F.: The second skin: ecological role of epibiotic biofilms on marine organisms, Front. Microbiol., 3, 1–21, 2012.

Webb, A. P. and Eyre, B. D.: Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification, Mar. Ecol.-Prog. Ser., 268, 205–220, 2004.

Webster, N. S. and Taylor, M. W.: Marine sponges and their microbial symbionts: love and other relationships, Environ. Microbiol., 14, 335–346, 2012.

Weisz, J. B., Hentschel, U., Lindquist, N., and Martens, C. S.: Linking abundance and diversity of sponge-associated microbial communities to metabolic differences in host sponges, Mar. Biol., 152, 475–483, 2007.

Welsh, D. T. and Castadelli, G.: Bacterial nitrification activity directly associated with isolated benthic marine animals, Mar. Biol., 144, 1029–1037, 2004.

Welsh, D. T., Dunn, R. J. K., and Meziane, T.: Oxygen and nutrient dynamics of the upside down jellyfish (*Cassiopea* sp.) and its influence on benthic nutrient exchanges and primary production, Hydrobiologia, 635, 351–362, 2009.

Wenzhöfer, F. and Glud, R. N.: Small-scale spatial and temporal variability in coastal benthic O_2 dynamics: effects of fauna activity, Limnol. Oceanogr., 49, 1471–1481, 2004.

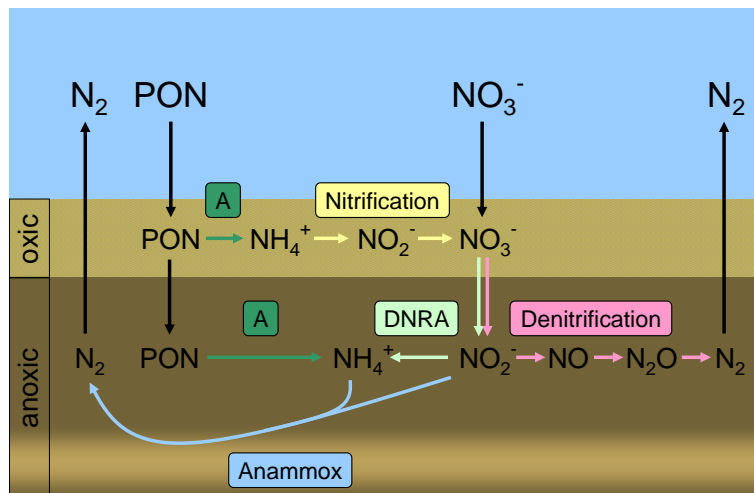**Stimulation of microbial nitrogen cycling in aquatic ecosystems**

P. Stief

Title Page

Abstract | Introduction

Conclusions | References

Tables | Figures

◄ | ►

◄ | ►

Back | Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 1. Macrofauna-induced stimulation of benthic nitrification and denitrification and of ammonium and nitrate fluxes across the sediment–water interface.

	Stimulation factor (x-fold)				Absolute change of flux ($\mu mol\,N\,m^{-2}\,h^{-1}$)		Total DIN flux ($\mu mol\,N\,m^{-2}\,h^{-1}$)	
	Nitrification	Denitrification	NH_4^+-Flux	NO_3^--Flux[*]	NH_4^+-Flux	NO_3^--Flux	Control	Animals
Minimum	1.0	0.3	0.1	0.3	+5	−1698	−558	−850
Maximum	9.0	7.0	15.4	9.6	+1263	+530	+246	+1156
Average	**3.0**	**2.4**	**5.3**	**2.2**	**+235**	**−18**	**+24**	**+162**
SD	2.3	1.5	4.1	2.2	285	381	158	372
N	15	39	26	14	31	28	27	27

Stimulation factors, absolute changes of fluxes, and total DIN fluxes were calculated based on the data presented in Fig. 4. Note that the number of studies (*N*) varies between the different factors because the individual studies provided different subsets of information needed for the calculations.
[*]Stimulation factor was only calculated for cases in which the NO_3^--flux was directed into the sediment in both the presence and absence of macrofauna.

Fig. 1. The benthic microbial nitrogen cycle in aquatic ecosystems. Black arrows indicate transport of particles or solutes between water and sediment; colored arrows indicate conversions along individual nitrogen-cycle pathways. PON: Particulate Organic Nitrogen, A: Ammonification, DNRA: Dissimilatory Nitrate Reduction to Ammonium, Anammox: Anaerobic ammonium oxidation. Boxed labels on the left demarcate oxic and anoxic layers within the sediment. To simplify matters, the pathway Nitrogen fixation ($N_2 \rightarrow NH_4^+$) is omitted.

A

Ventilation

oxic
anoxic
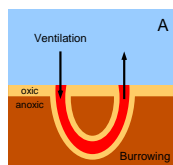
Burrowing

Ecosystem engineering by sediment infauna

• Physical-chemical alteration of habitat

  • Extension of oxic-anoxic interface due to burrowing and ventilation

  • Provision of dynamically oxic-anoxic microenvironments due to ventilation, respiration, and excretion

    → Modified resource supply to sediment bacteria

   → Enhanced organic matter mineralization, coupled nitrification-denitrification, and ammonium release

B
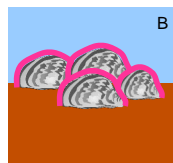
Ecosystem engineering by reef-building epifauna

• Physical-chemical alteration of habitat

  • Extension of surface area for microbial colonization due to biogenic structures

  • Enrichment of organic matter due to biodeposition

    → Modified resource supply to benthic microorganisms

    → Enhanced organic matter mineralization, nitrification and denitrification, and ammonium release

C

Deposit-feeding
Biofilm scraping
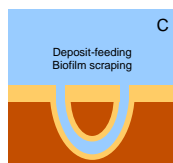
Grazing

• Ingestion of free-living and particle-attached bacteria

  • Decline in abundance of slow-growing bacteria

  • Decline in metabolic activity of grazing-sensitive bacteria

    → Reduced nitrification activity at the sediment surface

D
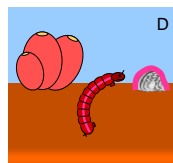
Symbiosis

• Intimate organismic association of bacteria and macrofauna in exoskeletal biofilms, gut contents, and soft tissues

  • Provision of dynamically oxic-anoxic microenvironments within host organism

  • Supply of metabolic waste products from host to symbiont

    → Distinct benthic compartments for many different nitrogen cycle pathways

    → Nitrous oxide production due to animal-associated nitrification and denitrification

Fig. 2. Three types of animal–microbe interactions that interfere with benthic nitrogen cycling in aquatic ecosystems: **(A)** and **(B)** ecosystem engineering, **(C)** grazing, and **(D)** symbiosis. The site of the microbial activity of interest is highlighted in pink color (**(A)** sediment burrow, **(B)** surface of biogenic reef structures, **(C)** sediment surface, **(D)** soft tissues, gut, and shell biofilm). Drawings of animals and biogenic structures are stylized and not to scale.
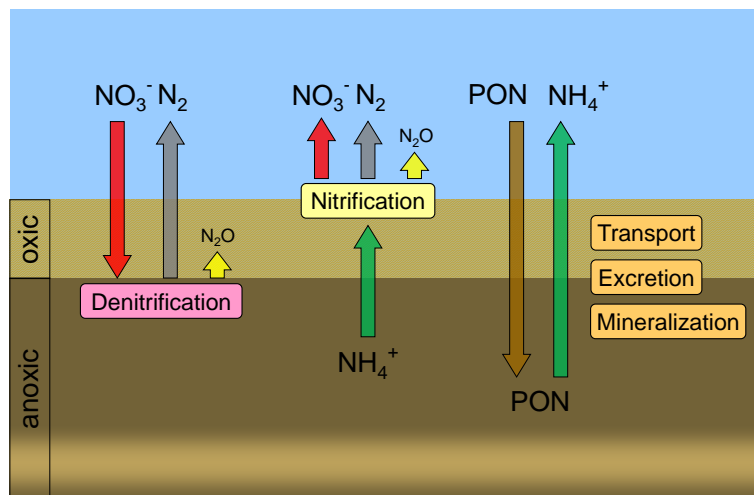
Fig. 3. Stimulation of N-cycle processes by benthic macrofauna and implications for fixed nitrogen removal and nitrous oxide emission. Block arrows indicate flux of particles (PON) or solutes (DIN) between sediment and water column. Length of arrows symbolizes size of flux; nitrous oxide fluxes, however, are shown as arrows of arbitrarily small size. Stimulation of denitrification and nitrification potentially removes fixed nitrogen as dinitrogen and increases nitrous oxide emission, while stimulation of PON mineralization, excretion of ammonium, and ventilation-enhanced transport of ammonium do not.

Fig. 4. (Caption on next page.)

Fig. 4. Data from 38 published studies in which **(A)** nitrification rates, **(B)** denitrification rates, **(C)** ammonium fluxes, and **(D)** nitrate fluxes were compared between sediment with and without certain macrofauna species. Data were extracted from tables, figures, and the text of the published articles. Average rates and fluxes are given for sediment without macrofauna (Control) and sediment with the highest density of macrofauna (Animals) and were re-calculated to μmol N m^{-2} h^{-1}. Positive fluxes are directed from sediment to water column, negative fluxes are directed from water column to sediment. If no bar is displayed, then information was not available. Numbers behind species name indicate (i) animal density in individuals m^{-2} and (ii) the reference from which data were taken. NA = information not available.