

**CURRENT EVIDENCE****A case for addressing the unresolved role of permeable shelf sediments in ocean denitrification**Emily J. Chua <sup>1,\*</sup> Markus Huettel <sup>2</sup> Katja Fennel <sup>3</sup> Robinson W. Fulweiler <sup>1,4</sup><sup>1</sup>Department of Earth & Environment, Boston University, Boston, Massachusetts; <sup>2</sup>Department of Earth, Ocean, and Atmospheric Science, Florida State University, Tallahassee, Florida; <sup>3</sup>Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, Canada; <sup>4</sup>Department of Biology, Boston University, Boston, Massachusetts**Scientific Significance Statement**

Human activities release vast amounts of reactive nitrogen, profoundly influencing the functioning of marine ecosystems. On the inner shelf, where these effects are most pronounced, sediments have emerged as potential hotspots of reactive nitrogen removal—and they are therefore increasingly thought to play a key role in the ocean nitrogen cycle. Despite their potential importance, shelf sediments are still overlooked in global models of ocean nitrogen and carbon cycles, limiting model accuracy and predictive power. Through analysis of recent work, we identified unresolved questions and controversies, and propose a three-pronged approach to improve our mechanistic understanding and modeling of nitrogen removal on the continental shelf and in the global ocean.

**Abstract**

The marine nitrogen cycle is a main driver of ocean productivity and affects global climate. Despite decades of study, we still have an incomplete understanding of the role of the marine nitrogen cycle in the Earth system. While marine sediments play a major role in nitrogen cycling in the ocean, magnitudes and mechanisms are largely unconstrained. Recent research suggests that permeable sandy sediments on the highly energetic and dynamic continental shelf are key components of the marine nitrogen cycle, but data to quantify their contribution are lacking. Here, we use insights from measurements and modeling studies to substantiate the hypothesis that shelf sediments are an overlooked driver of the marine nitrogen cycle. Specifically, we propose that permeable shelf sediments are sites for intense nitrogen conversions and suggest a three-pronged approach to address unresolved controversies.

The continental shelves play a disproportionate role in global biogeochemical cycling. While they occupy only 8% of the ocean's area (Hall 2002), they account for approximately 20% of marine primary production (Jahnke 2010). The inner

shelf (< 50 m depth) alone is the site of about 48% of the global flux of organic carbon to the seafloor (Dunne et al. 2007). Recent investigations emphasize that shelf sediments act as bioreactors that can efficiently convert carbon

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and nutrients (Seitzinger et al. 2006; Jahnke 2010; Bauer et al. 2013; Huettel et al. 2014). However, most prior research has focused on organic matter and nutrient cycling in the water column of the shelf, leaving the role of their sediments largely unconstrained. Many ocean carbon and nutrient cycling models and budgets do not adequately include shelf sediments, leaving out a substantial component of the marine nitrogen cycle.

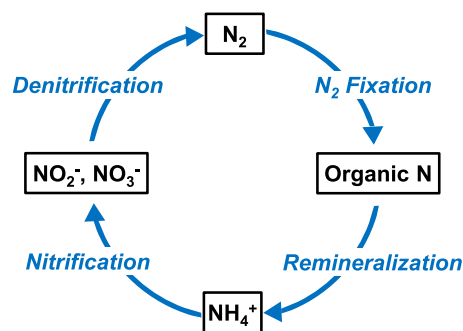
One distinctive characteristic of the shallow shelf is the abundance of highly permeable sands that cover at least 50% of continental shelves globally (Emery 1968; Hall 2002). Despite the prevalence of permeable sands, most research on shelf sediments to date has been conducted in fine-grained deposits. Fine-grained sediments may have a higher content of organic matter and reactants—the fuel for mineralization processes—while surficial sands typically contain low standing stocks of these substances. Sands were therefore thought to be “geochemical deserts.” Yet, there is an emerging consensus: the high permeability of well-sorted sands permits rapid pore-water exchange that transports organic matter into the seabed where it is swiftly processed and nitrogen subsequently remobilized. Permeable sediments may thus be hotspots of biogeochemical activity and undervalued in present models of the marine and global nitrogen cycles.

In the ocean, reactive nitrogen (Box 1) limits marine primary productivity and subsequent trophic level production. Furthermore, nitrogen availability is essential for carbon dioxide uptake and sequestration in the deep ocean via the biological pump. On the continental shelf, terrestrial runoff and atmospheric deposition are the major sources of reactive nitrogen from anthropogenic sources, with rivers delivering 40–66 Tg N yr<sup>-1</sup> and atmospheric deposition adding 8.5 Tg N yr<sup>-1</sup> (Voss et al. 2013). The open ocean laterally transports another 450–600 Tg N yr<sup>-1</sup>, while nitrogen-fixing organisms in shelf waters contribute about 17 Tg N yr<sup>-1</sup>. These numbers have high uncertainties, and recent discoveries of major marine microbial nitrogen fixers have prompted yet more questions concerning the magnitudes of nitrogen sources and sinks, and factors controlling process rates (Zehr and Capone 2020). Given that the marine nitrogen and carbon cycles are inextricably linked, our limited grasp of the first obscures our conception of the second, undermining our ability to predict future climate change (Gruber and Galloway 2008). As humans fundamentally alter the nitrogen cycle, better understanding its role in the earth system is essential to prevent further deterioration of the marine and global environment.

Most estimates of the marine nitrogen budget (Box 1) are bracketed by large uncertainties. We posit that a substantial fraction of this uncertainty is due to the present lack of measurements and mechanistic understanding of processes occurring in a largely overlooked environment: permeable shelf sediments. A small but growing body of work has begun to focus on nitrogen cycling in shelf sands, motivated by the

### Box 1. Marine nitrogen budget.

Nitrogen (N) exists in many chemical forms, and its cycling is governed by several microbially mediated transformations that convert biologically inert dinitrogen gas (N<sub>2</sub>) to various fixed or reactive forms, including ammonium (NH<sub>4</sub><sup>+</sup>), nitrite (NO<sub>2</sub><sup>-</sup>), and nitrate (NO<sub>3</sub><sup>-</sup>). In the simplified nitrogen cycle depicted, N<sub>2</sub> dissolved in the water column is taken up by microbes and fixed to organic N (N<sub>2</sub> fixation). Organisms consume and break down the organic N, releasing NH<sub>4</sub><sup>+</sup> (rem mineralization). Other microbes convert NH<sub>4</sub><sup>+</sup> to NO<sub>2</sub><sup>-</sup>, and then to NO<sub>3</sub><sup>-</sup> (nitrification). To complete the cycle, microbes convert nitrate back to N<sub>2</sub> (canonical denitrification). To first order, the inventory of reactive N is controlled by denitrification (defined here as any process that results in loss of fixed nitrogen from the biosphere; Devol 2008) and N<sub>2</sub> fixation (Gruber 2008). Whether the marine nitrogen budget is balanced remains controversial (Zehr and Capone 2020): estimates either find that losses outweigh sources (Galloway et al. 2004; Codispoti 2007; Voss et al. 2013), or that the budget is approximately balanced (Gruber 2008; Wang et al. 2019).



central question of whether they are sites of significant nitrogen removal via denitrification. Here, we synthesize recent work on denitrification in shelf sands, highlight unresolved controversies, and evaluate potential changes to shelf nitrogen cycling in the face of increasing human perturbations to the ocean.

### Changing perceptions

In general, waves and currents sort shelf sediments into a gradient from organic-poor sand beds on the inner shelf to fine-grained sediments richer in organic matter in the mid and deeper shelf (McCave 2002; Fig. 1). Episodic major storm events temporarily—yet profoundly—alter this gradient through the mobilization of decimeter-thick surface sediment

layers, deep sediment oxygenation, and the redistribution of organic matter and nutrients (Scavia et al. 2002; Osburn et al. 2019; Paerl et al. 2020). In the last three decades, studies focusing on transport and diagenetic reactions (i.e., physical and chemical processes that alter sediments after deposition) in inner shelf sands suggest they play an underappreciated role in biogeochemical cycling. This work was stimulated by early experiments in shallow permeable environments that revealed the effectiveness of water flow through the interconnected pore spaces in transporting reactants into and out of sand beds (Webb and Theodor 1968; Thibodeaux and Boyle 1987). This conveyor-belt like advective transport of substrates can accelerate microbial decomposition processes, transforming sand beds into biocatalytical converters, analogous to trickling bed filters in water treatment (Huettel et al. 2014).

Advective exchange in shelf sands is driven by physical processes operating over distances of millimeters to kilometers and over time frames spanning seconds to years (Santos et al. 2012b). This exchange consequently affects the cycling of nitrogen over a wide range of spatial and temporal scales. The largest driver of advective exchange may be the circulation induced by the interaction of bottom flows with seabed topography, which can drive water through the upper 5–50 cm of rippled sand beds (Santos et al. 2012b). Advective transport scales with the direction and strength of bottom currents, as well as with ripple dimensions, resulting in a highly dynamic, four-dimensional environment for sedimentary nitrogen cycling processes. Key parameters governing sedimentary denitrification—including temperature, bottom currents, sediment–water exchange, redox oscillations, sedimentary nitrate concentrations, benthic production, and organic content—may reach highest values in the inner and mid shelf (Fig. 1). We hypothesize that the zone of maximum benthic denitrification is therefore located within the upper section (< 100 m) of the shelf.

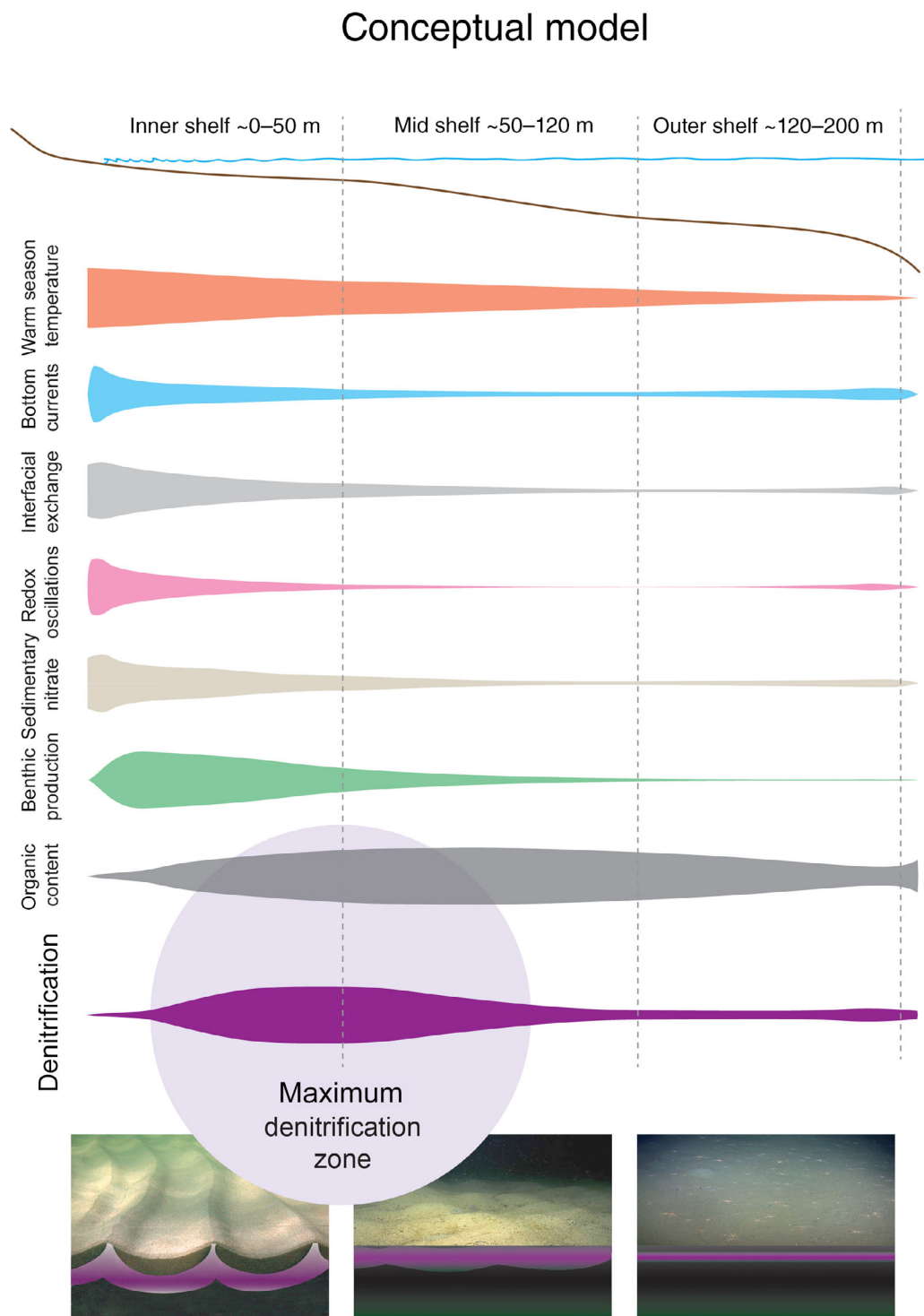
At present, the intricate links between biogeochemical reactions within the sand and boundary layer hydrodynamics are not well understood due to limited in situ measurements. The tight coupling between pore-water flow and ensuing reactions makes quantification of the latter challenging, and measurement methods must consider variable environmental drivers. Moreover, denitrification is a particularly difficult process to measure, as its dominant end product ( $N_2$ ) has a high ambient concentration in the environment. Only over the past 15 yr have studies taken transport into account when attempting to constrain nitrogen loss in permeable sediments (Fig. 2; Table 1). While still small, this ground-breaking body of work has challenged our present notions of nitrogen cycling on the shelf by calling into question results that ignore the dynamic contributions of the benthic environment and permeable sediments. These studies include experiments that attempt to induce realistic pore-water flows in the laboratory, novel in situ methods (benthic chambers and aquatic eddy covariance instruments), and model simulations of advective flow-driven reactions. Methods to generate advective flow are percolated

cores, or sediment incubation devices pumped with water (Rao et al. 2007; Gao et al. 2010; Santos et al. 2012a; Evrard et al. 2013; Marchant et al. 2016), and chambers with stirred overlying water (Eyre et al. 2008; Gihring et al. 2010), which can be used in situ or ex situ. The eddy covariance method was first adapted for use underwater by Berg et al. (2003) and enables noninvasive measurements of fluxes across the sediment–water interface. Models of permeable sediments extend the 1D diffusive framework of traditional diagenetic models (Box 2) to accommodate 3D advective flow. Specifically, they calculate pore-water flow fields from pressure gradients at the sediment–water interface and combine these with a reactive transport scheme for the coupled chemical reactions that govern nitrogen biogeochemistry (Cook et al. 2006; Cardenas et al. 2008; Kessler et al. 2012, 2013; Azizian et al. 2015). The results from these laboratory, nearshore, and small-scale modeling studies imply that realistic regional models of the nitrogen conversions in inner shelf sands require reliable information on in situ advective transport for calculating reaction rates. When hydrodynamic regime and physical sediment characteristics are known, models can provide some of the pore-water transport information (Shum 1992; Cardenas et al. 2008). However, existing models have so far only been tested at small scales (on the scale of sand ripples, i.e., meters) and therefore represent idealized cases. Furthermore, validation of model results through in situ measurements is largely missing.

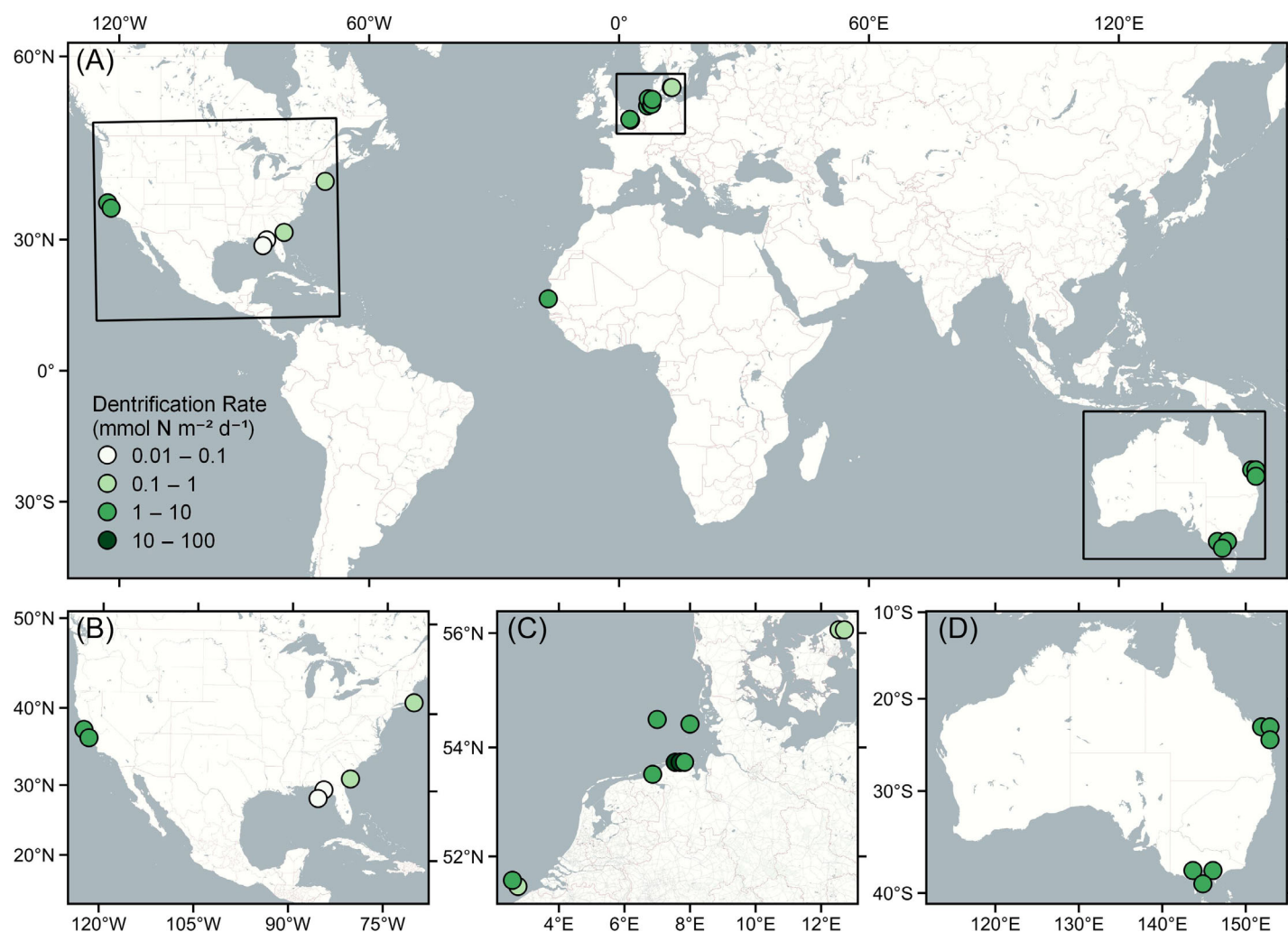
Regional models of permeable sediments that include the dynamics of key environmental drivers are computationally demanding, and their expansion to even modest scales of tens to hundreds of kilometers presently is prohibitive. In existing regional and large-scale biogeochemical models (Box 2), sediments are typically represented by relatively simple parameterizations that can be based on stoichiometric arguments (Fennel et al. 2006), multivariate fits to observations (Bohlen et al. 2012), or output from diagenetic models through the meta-model approach (Laurent et al. 2016). Only recently have diagenetic models been coupled directly to regional biogeochemical models (Moriarty et al. 2018, 2020). However, neither the meta-model approach nor the direct coupling of diffusion-dominated diagenetic models represents permeable sediments well. We therefore require a better mechanistic representation of biogeochemical processing in permeable sediments, and a method to generalize these processes over the shelf scale. To achieve these aims, we must obtain knowledge of spatiotemporally varying parameters such as wave action, sediment permeability, and large-, and small-scale topography. Efforts should also be devoted to improving quantitative approaches for scaling up.

### Unresolved controversies

The recent body of work on transport and reaction in permeable sands has unearthed many questions about nitrogen



**Fig. 1.** Hypothesized conceptual model depicting key factors that control denitrification in shelf sediments and a hypothetical zone of maximum benthic denitrification. Top: Shelf depth profile, divided into inner, mid and outer shelf regions. Rows 2–7: Hypothetical influence of key environmental factors controlling denitrification (i.e., temperature (Nowicki 1994; Cornwell et al. 1999), sediment–water exchange (Santos et al. 2012b), redox oscillations (Aller 1994; Huettel et al. 1998; Sun et al. 2002; Skoog and Arias-Esquivel 2009), nitrification (Seitzinger and Giblin 1996), and availability of nitrate and organic matter (Nowicki 1994; Cornwell et al. 1999; Fulweiler and Heiss 2014)) in the different shelf regions. Purple circle: The assumed region of maximum sedimentary denitrification, which is located where the cumulative effect of the main controls of benthic denitrification is strongest. Bottom: Cross sections of the seabed in the three shelf regions, with permeable sands, muddy sands, and fine-grained deposits dominating the sediments of the respective regions; purple shading depicts the sedimentary denitrification zone.



**Fig. 2.** Locations of studies that have measured or modeled denitrification rates in permeable shelf sediments: (A) worldwide, (B) in the United States, (C) in Northern Europe, and (D) in Australia. Studies at the same or similar sites are staggered for visualization. If a study reported a range of denitrification rates and not an overall mean, then the midpoint was calculated from the range given. See Table 1 for the exact rates and method used in each study.

cycling in permeable sediments. Central to these inquiries is whether significant denitrification occurs in permeable shelf sands. The conventional view of benthic biogeochemistry assumes that denitrification occurs primarily in fine-grained sediment, which are rich in organic matter—the fuel for denitrification—and low in oxygen, as opposed to permeable sediments, which are poor in organic matter and better oxygenated. Indeed, a recent study on nitrogen cycling across a wide permeability gradient on the Northeast Atlantic Shelf (Toussaint et al. 2021) found that low permeability sediments with a high organic matter content create a more favorable environment for denitrifiers. However, our revised understanding that surface topography/flow interactions efficiently supply reactants in permeable sediments implies that the ensuing dynamic and enhanced interfacial area between oxic and anoxic zones could promote nitrite and nitrate

production via nitrification, which in turn feeds denitrification. In other words, permeable sands should act as bioreactors rather than biogeochemical deserts.

At present, the handful of experimental and modeling studies available disagree whether denitrification rates in sands are higher or lower than in fine-grained sediments, and hence whether sands are more efficient at processing reactive nitrogen. For example, a study conducted in subtidal quartz sands in the Gulf of Mexico found a near-complete conversion of remineralized nitrogen to  $\text{N}_2$ , indicating that these sands are effective sites of denitrification (Gihring et al. 2010). These results are supported by other experimental studies that found high denitrification rates in tropical carbonate sands (Eyre et al. 2013), and temperate silica sands from the Wadden Sea, Northern Europe (Gao et al. 2012; Marchant et al. 2016). In contrast, results of modeling studies have



**Table 1.** Compilation of denitrification rates measured in permeable sediments on the continental shelf to date. The mean denitrification rate is the value plotted in Fig. 1. Only studies that accounted for advective flushing were included; see the Supporting Information for flushing rate calculations. NR, not reported; GC-IRMS, gas chromatography coupled to isotope ratio mass spectrometry; MIMS, membrane inlet mass spectrometry.

Reference	Location	Rate range (mmol N m <sup>-2</sup> d <sup>-1</sup> )	Rate mean (mmol N m <sup>-2</sup> d <sup>-1</sup> )	Flushing rate (L m <sup>-2</sup> d <sup>-1</sup> )	Method
<i>Inner shelf (0–50 m)</i>					
Braeckman et al. (2014)	Southern North Sea	0–1.80	NR	NR	Ex situ stirred chambers; N <sub>2</sub> :Ar ratios measured with MIMS
Cardenas et al. (2008)	Martha's Vineyard Coastal Observatory, MA, USA	<0.24–0.72	0.48	16–164	Reactive transport model
Cook et al. (2006)	Beach near Marine Biological Lab in Helsingør, Denmark	0.048–3.74	0.48	3.5–87	Reactive transport model
Cook et al. (2006)	Beach near Marine Biological Lab in Helsingør, Denmark	1.68–3.12	0.48	5.3–90	Stirred chambers (ex situ); N <sub>2</sub> :Ar ratios measured with MIMS
Evrard et al. (2013)	Port Phillip Bay, Victoria, Australia	0.018–4.5	NR	953	Percolated cores; isotope pairing measured with an elemental analyzer coupled to IRMS
Gao et al. (2010)	Janssand sand flat, Wadden Sea	4.5–11.3	7.2	113	Percolated cores, slurry incubations, stirred bioreactor; isotope pairing measured with GC-IRMS, nitrate measured with micro-sensors; N <sub>2</sub> (aqueous gas) measured directly with MIMS
Gao et al. (2012)	East Frisian Wadden Sea	3.4–25.3	4.8	NR	Percolated cores and slurry incubations; isotope pairing measured with GC-IRMS
Gihring et al. (2010)	Apalachicola Bay	<0.001–0.011	NR	NR	Ex situ stirred chambers; N <sub>2</sub> :Ar ratios measured with MIMS
Gihring et al. (2010)	Gulf of Mexico	0.035–0.099	NR	NR	Ex situ stirred chambers; N <sub>2</sub> :Ar ratios measured with MIMS
Johnson et al. (2011)	Half Moon Bay, central California continental shelf		3.98	NR	Eddy correlation; nitrate fluxes measured with a modified In Situ Ultraviolet Spectrophotometer optical nitrate sensor (Johnson and Coletti 2002)
Johnson et al. (2011)	Point Sur, central California continental shelf		1.10	NR	Eddy correlation; nitrate fluxes measured with a modified In Situ Ultraviolet Spectrophotometer optical nitrate sensor (Johnson and Coletti 2002)

(Continues)

**Table 1.** Continued

Reference	Location	Rate range (mmol N m <sup>-2</sup> d <sup>-1</sup> )	Rate mean (mmol N m <sup>-2</sup> d <sup>-1</sup> )	Flushing rate (L m <sup>-2</sup> d <sup>-1</sup> )	Method
Kessler et al. (2012)	Brighton Beach, Victoria, Australia		1.6	15	Flume tank and reactive transport model; isotope pairing measured with GC-IRMS
Kessler et al. (2013)	Brighton Beach, Victoria, Australia		2.0	NR	Diffusion equilibrium thin layer (DET) gel technique used in a flume tank and reactive transport model; isotope pairing measured with GC-IRMS
Marchant et al. (2014)	East Frisian Wadden Sea	9.6–27.6	NR	86–252	Percolated cores; isotope pairing measured with GC-IRMS, N <sub>2</sub> (aqueous gas) measured directly with MIMS
Marchant et al. (2016)	South-East North Sea	0.52–2.28	1.2	252	Percolated cores; isotope pairing measured with GC-IRMS, N <sub>2</sub> (aqueous gas) measured directly with MIMS
Marchant et al. (2017)	East Frisian Wadden Sea	15.8–77.8	46.8	69	Percolated cores; isotope pairing measured with MIMS
Toussaint et al. (2021)	Southern North Sea	0–10	NR	2.12–24.92	Ex situ stirred chambers; DIN measured with colorimetry and used in a mass balance model
<i>Mid shelf (50–120 m)</i>					
Eyre et al. (2008)	Heron Island reef flat, Gladstone, Australia	0.82–11.5	NR	43 and 213	Benthic chambers (in situ); isotope pairing measured with GC-IRMS
Eyre et al. (2013)	Heron Island reef flat, Gladstone, Australia	1.4–7.3	NR	43	Benthic chambers (in situ); N <sub>2</sub> :Ar ratios measured with MIMS
Neumann et al. (2017)	German Bight	0.134–32	2.76	NR	Rhizon-sampled cores; nitrate concentrations measured with nutrient autoanalyzer
Rao et al. (2007)	South-Atlantic Bight, New Jersey continental shelf	0.25–1.4	NR	316	Percolated cores; N <sub>2</sub> :Ar ratios measured with MIMS
Santos et al. (2012a)	Heron Island, Great Barrier Reef	0.3–8.1	3.6	744–6000	Percolated cores; N <sub>2</sub> :Ar ratios measured with MIMS
Sokoll et al. (2016)	North-West African Shelf	1.31–9.15	3.6	NR	Slurry incubations; isotope pairing measured with GC-IRMS

### Box 2. Biogeochemical models and permeable sediments.

Biogeochemical models represent biogeochemical properties and processes using a mathematical formalism to simulate standing stocks of these properties and the fluxes between them. Such models can be analytical or numerical; can represent a steady state or be time dependent, deterministic, or stochastic; and can be spatially explicit or averaged in space. All models require constant or time-dependent input parameters in some form including rate constants, environmental properties, and initial and boundary values.

Here, we distinguish between biogeochemical ocean models that are primarily focused on the water column overlying marine sediments, referred to as 3D regional and global biogeochemical models, and models of these sediments, referred to as diagenetic models. Among the diagenetic models, we distinguish between spatially explicit, time-dependent models, and space- and time-averaged models, referred to as parameterizations.

**A. 3D regional and global biogeochemical models:** These spatially explicit, time-dependent models are coupled to hydrodynamic models that simulate ocean circulation and describe the distribution and transformations of biogeochemical properties in the water column. They are subject to the same circulation processes as seawater and to additional transformation processes represented by empirical parameterizations. These models typically ignore sediments or represent them relatively crudely (see C below), although there are recent attempts to couple a diagenetic model to a 3D regional model that also consider sediment resuspension and transport (Moriarty et al. 2018, 2020). Regional and global biogeochemical models that ignore marine sediments are likely to significantly underestimate sediment denitrification and thus misrepresent regional to global nitrogen transformations/budgets.

**B. Diagenetic models:** Most of these models are based on a 1D diffusive framework that represent the sediment as horizontally homogenous layers in which particulate matter and pore-water solutes are explicitly represented. Advection, if accounted for at all, refers to slow burial or is implicitly represented by large diffusivities in the upper layers of the model. While these models work well for clays and muds, they do not appropriately represent permeable sediments because they neglect advective flow, which is fundamental to the latter's biogeochemical functioning. Building on pioneering contributions by Shum (1992, 1993, 1995), novel modeling work on permeable sediments

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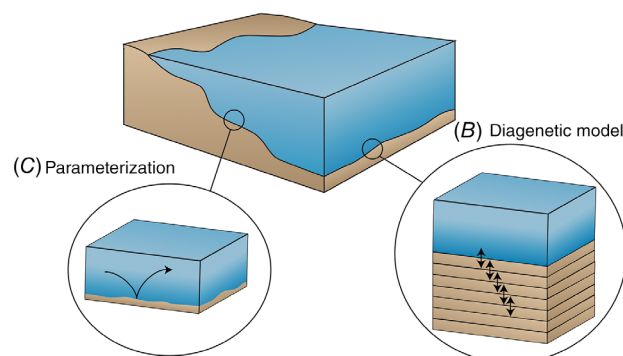
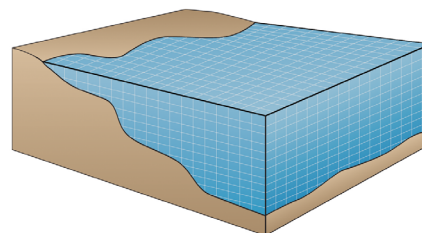
### Box 2. Biogeochemical models and permeable sediments.—cont'd

by Cardenas et al. (2008), Cardenas and Wilson (2007a,b), and Meysman et al. (2007) showed the importance of turbulence and oscillatory flows for diagenetic modeling of sands. These models represent the 3D structure of sediments in idealized settings on the scale of multiple sand ripples and are forced by advective flows. Because they are highly localized and computationally demanding, these permeable sediment models cannot presently be scaled up to regional scales of tens to hundreds of kilometers.

**C. Sediment parameterizations:** This group of approaches does not explicitly represent sediments and the physical transport and biogeochemical transformation processes within them. Instead, they are functional relationships that assume steady state exchange between the sediments and overlying water column and can be approximated independently of location if a set of input parameters is known.

Except for the idealized and localized models of permeable sediments described in B, none of the above represent processes in permeable sediments well. Where diagenetic models have been employed in conjunction with 3D regional or global models, either as the basis for the meta-model approach or directly coupled to the water-column model, the 1D diffusive framework for cohesive sediments was used.

(A) 3D regional biogeochemical model





suggested that sands remove only a small amount of reactive nitrogen via denitrification relative to fine-grained sediments (Cook et al. 2006; Cardenas et al. 2008; Kessler et al. 2013; Azizian et al. 2015). According to these studies, advective flows can transport the remaining reactive nitrogen to the overlying water, causing permeable sand beds to act as a net source of reactive nitrogen.

Another well-established paradigm, the redox cascade, states that microbial communities use electron acceptors to oxidize organic matter following a sequence of high-to-low energy yield. Denitrifiers were thought to only use nitrite and nitrate as alternative electron acceptors once oxygen had been depleted—therefore, denitrification is viewed as a strictly anaerobic process that only occurs in a distinct horizontal sediment layer below the oxygenated sediment surface layer (i.e., upper millimeters). Moreover, oxygen was thought to repress expression of the denitrification pathway (Bergaust et al. 2012). Yet, several experimental studies using intertidal and subtidal sands from the South Atlantic Bight (Rao et al. 2007, 2008) and the Wadden Sea (Gao et al. 2010; Marchant et al. 2017) have observed high rates of  $N_2$  production under oxic conditions. One explanation for this so-called aerobic denitrification is as follows. As currents remobilize the sand bed, the shifting sediment topography varies the oxygen penetration depths and exposes freshly buried organic matter to anoxic and oxic conditions. In tidal systems with rapidly fluctuating redox conditions, it may therefore be favorable to constantly express multiple respiratory pathways to capitalize on the variety of energy sources available—in other words, denitrifiers may have adapted to simultaneously use oxygen and nitrate (Gao et al. 2010; Marchant et al. 2017). Aerobic denitrification may not be a universal phenomenon (Evrard et al. 2013), but could also arise due to temporary anoxic microniches in oxic sediment, as suggested for the water column (Bianchi et al. 2018).

It is also unclear whether other environmental parameters such as bottom water nitrate concentrations are important in driving denitrification rates in submerged sands. Denitrification can either be fueled by nitrate from the overlying water (direct denitrification), or nitrate produced in the sediment (coupled nitrification–denitrification). Measurements in different shelf environments have found that the supply of nitrate from the overlying water may not always drive permeable sediment denitrification. At certain sites, coupled nitrification–denitrification is an important nitrogen loss pathway (South Atlantic Bight, southeast US shelf, Rao et al. 2008; Wadden Sea, northwest European shelf, Gao et al. 2012; German Bight, northwest European shelf, Marchant et al. 2016); at sites where transport predominates over reaction rates, nitrate may pass through the system without much effect on sedimentary denitrification (northwest Africa shelf; Sokoll et al. 2016). On the other hand, reactive transport models suggest that in some environments with permeable sea beds, the majority of denitrification is fed by nitrate from overlying water (Kessler

et al. 2012, 2013). These modeling studies predict that during periods with no bedload transport and stationary ripples, upward pore-water flow through a “redox chimney” at ripple peaks causes ammonium release from deeper, anoxic sediments to the overlying water, allowing it to bypass nitrification in the surface oxic zone. Therefore, the models suggest that the coupling between nitrification and denitrification in stationary sand beds is weak and direct denitrification dominates. Given these recent measured and modeled results, the influence of bottom water nitrate on permeable denitrification rates likely depends on the ambient flow regime.

These controversies have practical implications in terms of modeling denitrification at shelf and global scales, and hence for estimating the marine nitrogen budget. The most recent estimates of this budget find that marine nitrogen loss via denitrification exceeds known inputs by 60–234 Tg N yr<sup>−1</sup> (Codispoti et al. 2001; Codispoti 2007; Voss et al. 2013). This imbalance largely owes to a high benthic denitrification rate, which in turn is based on sparse observations of denitrification in shelf sediments. If denitrification rates in shelf sands are lower than in finer-grained sediments, it might explain the apparent imbalance in the global nitrogen budget. Substantial denitrification in these sands as suggested by recent findings, on the other hand, would further increase the imbalance. If denitrification can be parameterized with easily measured factors such as water column nitrate and/or oxygen concentrations, then models might be used to predict rates. For example, a recent model used water column nitrate and phosphate concentrations to estimate global patterns of denitrification rates (Wang et al. 2019). Yet, as summarized above, some studies have found that nitrate and/or oxygen concentrations are not the primary or exclusive control of denitrification rates in sands, confounding efforts to take this approach. If this is truly the case, then models of nitrogen loss in shelf sediments that commonly rely on sediment oxygen consumption as a proxy for denitrification (Fennel et al. 2006) may have to be revised. If anaerobic microenvironments exist in the aerobic layer of permeable sediments, either in organic particles (Jahnke 1985) or intragranular spaces in carbonate sands (Kessler et al. 2014), approaches like Bianchi et al. (2018)’s—which represents anaerobic microenvironments in sinking particles in a globally applicable parameterization for water-column denitrification—may prove useful. Furthermore, if denitrification rates are governed not only by reaction kinetics but also by metabolic responses to changing electron acceptors, then this feature should be incorporated into reactive transport models.

### *Fate in a changing environment*

Our understanding of permeable shelf sediment nitrogen dynamics is rudimentary, and our knowledge of how they will respond to climate change and other anthropogenic forcings

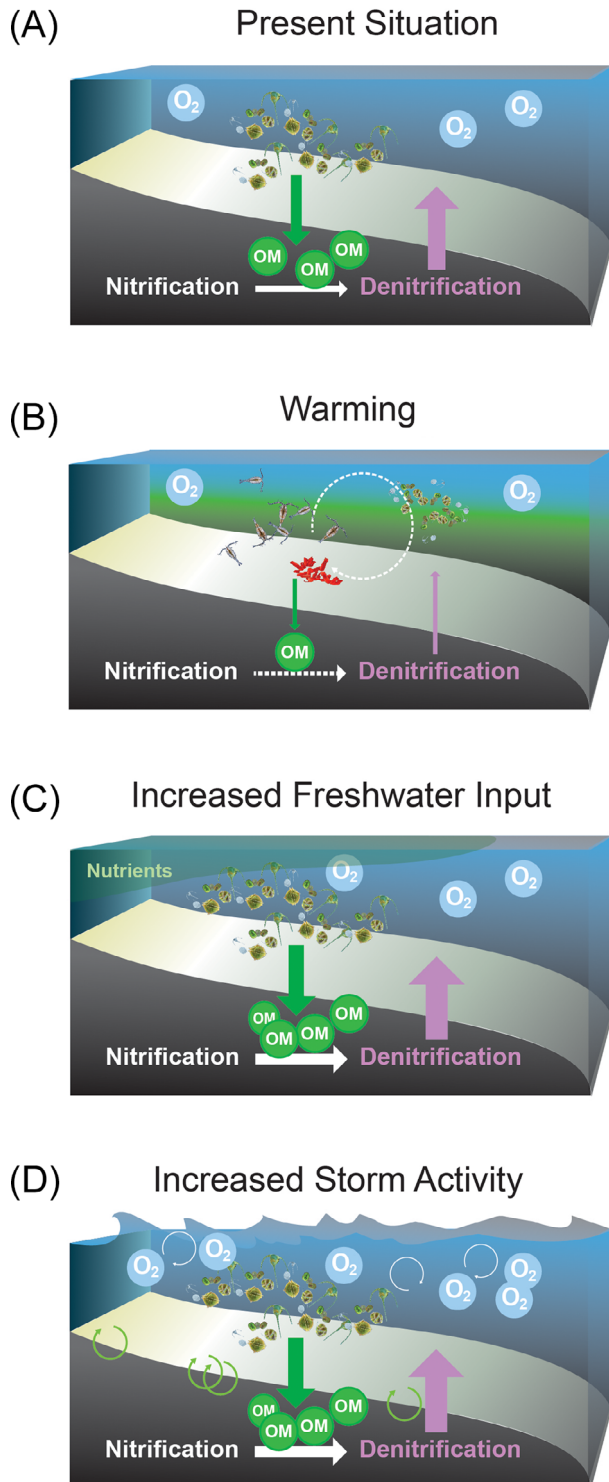
is even more limited. Here, we hypothesize plausible scenarios largely based on studies from impermeable marine sediments.

Ocean water temperatures are increasing globally as are occurrences of extreme heat events (Bronsealer and Zanna 2020; Chen et al. 2015; Liu et al. 2016). We anticipate

that elevated water temperature will lead to a series of physical, chemical, and biological changes that could have negative as well as positive effects on permeable shelf sediment nitrogen cycling (Fig. 3).

Warming water temperatures are leading to global decreases in water column oxygen concentrations (Breitburg et al. 2018). Increasing hypoxia may limit coupled nitrification–denitrification, a potential dominant pathway of nitrogen removal in permeable shelf sediments. Second, warming will increase stratification of the shelf water column, ultimately lowering organic matter deposition to the permeable shelf seafloor (Fields et al. 2014). This decrease in organic matter loading to the benthos may be exacerbated by warming-induced decreases in phytoplankton size (Morán et al. 2010), and overall declines in productivity (Gregg 2005; Boyce et al. 2010; Hofmann et al. 2011). Faster metabolic rates can lead to enhanced microbial and zooplankton grazing in the water column (Brown et al. 2004; Sommer and Lengfellner 2008). Thus, warming may decrease the quantity and quality of organic matter reaching permeable shelf sediments, subsequently limiting their “bioreactor” capabilities.

Changes in the timing and magnitude of freshwater inputs to shelf systems may increase stratification but will surely deliver more anthropogenic nutrients. Given the anticipated escalations in extreme precipitation events, we predict that extreme biogeochemical events on shelf environments may follow (Lu et al. 2020). Ensuing larger oscillations in the concentrations of reactive nitrogen, organic matter, and oxygen have the potential to boost sandy shelf sediment denitrification through enhancing spatial and temporal redox gradients and substrate supply. Predicted future changes in wind speeds and the severity of storm events (Young and Ribal 2019) similarly have the potential to enhance nitrogen cycling through increased mixing. Stronger winds result in higher waves, deeper mixing, and enhanced redistribution of dissolved oxygen, nutrients, organic matter, and sediments. Water column mixing induced by storm events could stimulate primary productivity, even on oligotrophic shelves (Chen et al. 2021).



**Fig. 3.** Hypothesized scenarios depicting how environmental changes caused by human activities could alter denitrification rates in shelf sediments. **(A)** Present situation. **(B)** Warming increases water column stratification, which reduces mixing and reoxygenation of the water column and may therefore lower rates of coupled nitrification–denitrification. Warming has also been linked to smaller phytoplankton cells and increased bacterial and zooplankton grazing, which may alter organic matter deposition to sediments and ultimately lower rates of benthic denitrification. **(C)** Increased freshwater inputs enhance terrestrial nutrient release to the ocean, stimulating phytoplankton production, and organic matter deposition, thereby increasing rates of sedimentary denitrification. **(D)** Increased wind speeds and storm severity temporarily enhance mixing and reoxygenation of the water column and promote sediment erosion/redeposition, stimulating coupled sediment nitrification–denitrification. Many other scenarios are possible.  $O_2$ , dissolved oxygen; OM, organic matter.

These examples outline some hypothetical scenarios that may be caused by the changing global climate, but a plethora of other developments is possible, some of which may be beyond our current imagination.

Predicting the future of continental shelf nitrogen cycling thus is challenging given the lack of data, but also due to the large ecological variety of shelf environments. One unifying framework for approaching studies of future change on continental shelves might be binning them by residence time, as Fennel and Testa (2019) suggest. In doing so, we can highlight areas that may be under threat from certain variables.

### **Moving forward**

Evidence is mounting that permeable sediments on continental shelves play a larger role in global biogeochemical cycling than previously thought. However, many global nitrogen budgets still do not even include sediments. To predict future changes in global biogeochemical cycles, we must resolve major uncertainties surrounding the nitrogen removal capacity of continental shelf sediments. These predictions are required now more than ever, given that reactive nitrogen from human inputs exceeds that from natural nitrogen fixation (Voss et al. 2013). This perturbation directly and indirectly contributes to climate change (Pinder et al. 2012), coastal eutrophication, harmful algal blooms, spreading of hypoxic zones (Diaz and Rosenberg 2008), and threatens coastal economies and important fisheries. Furthermore, it may alter the capacity of shelf sediments to process nitrogen.

As our activities continue to push the nitrogen cycle out of balance, pinning down the “ever faster moving target” (Gruber 2016) of the marine nitrogen budget is becoming increasingly challenging. To date, few studies have incorporated both transport and reaction in shelf sediments. Moreover, our sparse collection of studies (Fig. 2) has virtually all focused on temperate shelves; far more work is required in tropical carbonate sands and Arctic shelves.

We suggest three questions to focus future research on shelf sediments, and in particular, permeable shelf sediments:

1. How do anthropogenic influences (nitrogen loading, warming, acidification, oxygen decrease, and sea level rise) impact denitrification?
2. How does denitrification vary with spatial and temporal dynamics (at different latitudes and climates; upwelling shelves vs. river-dominated shelves; seasonal vs. episodic storm events)?
3. What are the present magnitudes and major trends of denitrification?

We propose a three-pronged approach to resolve these questions. First and foremost, we must increase the temporal and spatial resolution of in situ measurements in the inner shelf. These field observations are critical to providing a window into the rates, timing, and location of biogeochemical

processes in shelf environments and developing parameterizations for models. Novel in situ measurement techniques currently being developed for dynamic shelf sediments include aquatic eddy covariance instruments (Johnson et al. 2011; Huettel et al. 2020) and underwater mass spectrometers (Bell et al. 2012; Chua et al. 2021). The former can measure sediment-water fluxes of oxygen and nitrate in real time with no disturbances of sediment, light, or hydrodynamics. The latter can resolve multiple dissolved gas species simultaneously at high temporal resolution in the bottom water and within the sediment. Second, it is crucial to conduct laboratory experiments that investigate the transport-driven nitrogen cycling reactions in shelf sediments of different permeabilities under controlled conditions. These studies (Kessler et al. 2012; Marchant et al. 2017) will help us identify the key drivers of nitrogen cycling in permeable and fine-grained sediments, informing the design of field campaigns and providing validation for mechanistic models. Finally, we should further refine diagenetic models that incorporate the complex advective flow in sands (Cook et al. 2006; Cardenas et al. 2008; Kessler et al. 2013) and pursue modeling approaches that can extrapolate field measurements and small-scale model simulations to the shelf scale.

Because the inner shelf is such a dynamic environment, obtaining accurate field observations is a particularly challenging task—while measurement platforms such as gliders and moorings are increasingly being developed for the water column (Chai et al. 2020), we lack similar efforts to design technology to study marine sediments. Consequently, we must develop standardized sampling schemes and technology for simultaneously measuring hydrodynamic patterns and biogeochemical variables (e.g., solute/particle concentrations and fluxes) in sediments in diverse shelf environments and at multiple time scales. Lab and field observations, as well as data from small-scale models, are necessary to determine which factors are key to nitrogen cycling in shelf sediments. To make sense of these observations and data, critical parameters such as sediment type, permeability, bottom current dynamics, and flushing rate should be reported alongside rate data. We expect that the magnitudes and distribution patterns of key parameters affecting benthic denitrification on the shelf (Fig. 1) will change, which may alter the depth and the areal extent of the zone of maximum benthic denitrification. Predicting these changes is challenging, as the complexity of potential coastal ocean changes generates a spectrum of different scenarios.

Developing small-scale diagenetic models will allow us to obtain mechanistic insights into the biogeochemical functioning of permeable sediments, especially when combined with laboratory experiments that explore the impacts of likely drivers over a range of controlled conditions. For large-scale models, one can compare the biogeochemical processing that occurs due to advective pumping of reactants in permeable sediments to subgrid-scale processes in geophysical models of

atmosphere and ocean (e.g., cloud condensation, turbulent diffusion). Some processes cannot be explicitly resolved on large scales and thus must be parameterized. While it is possible to represent turbulent and oscillatory advective flow in permeable sediments through direct Large-Eddy Simulation modeling, doing so at scales of tens to thousands of kilometers will remain intractable for the foreseeable future. We advocate for a meta-model approach where tested process-based, small-scale models are used to derive parameterizations that can be used in large-scale models. The challenge, then, is to determine which factors best explain spatiotemporal variations in sediment biogeochemical processing and can be used as the input variables for such parameterizations. Some obvious candidates are water depth, wave action, bottom currents, sediment permeability, and large- and small-scale topography, but there are likely others that remain to be explored. Accurately representing dynamic biogeochemical inner shelf processes at the global scale poses considerable challenges—but doing so may reduce one of the largest sources of uncertainty in the global nitrogen budget.

Understanding and quantifying nitrogen cycling on the shelf are indispensable for designing global carbon and nutrient models and budgets. Accelerating human-induced changes to coastal and marine systems emphasize the urgency to develop adaptive models that permit a dynamic assessment of the consequences of the environmental changes for shelf and marine ecosystems. To develop these models, we require data from the inner shelf that, at present, are unavailable. Given our growing recognition of the importance of shelf sediments in global nitrogen cycling, we require a concerted effort to develop sensor systems for these environments. Improved measurement methods are fundamental to determining the role of continental shelf sediments in marine nitrogen cycling and predicting how it may change in the Anthropocene. In turn, obtaining a better knowledge of nitrogen cycling will advance our understanding of carbon cycling, and ultimately global climate.

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### Conflict of interest

The authors declare no competing interests.

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