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Microbial Nitrogen Cycling in Estuaries: From Genes to Ecosystem Processes

Julian Damashek[1,2] · Christopher A. Francis[1]

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Abstract Nitrogen (N) is one of the primary nutrients required to build biomass and is therefore in high demand in aquatic ecosystems. Estuaries, however, are frequently inundated with high concentrations of anthropogenic nitrogen, which can lead to substantially degraded water quality. Understanding drivers of biogeochemical N cycling rates and the microbial communities responsible for these processes is critical for understanding how estuaries are responding to human development. Estuaries are notoriously complex ecosystems: not only do individual estuaries by definition encompass gradients of salinity and other changing environmental conditions, but differences in physical parameters (e.g., bathymetry, hydrodynamics, tidal flushing) lead to a tremendous amount of variability in estuarine processes between ecosystems, as well. Here, we review the current knowledge of N cycling processes in estuaries carried out by bacteria and archaea, including both biogeochemical rate measurements and molecular characterizations of N cycling microbial communities. Particular attention is focused on identifying key environmental factors associated with distinct biogeochemical or microbial regimes across numerous estuaries. Additionally, we describe novel metabolisms or organisms that have recently been discovered but have not yet been fully explored in estuaries to date. While the majority of research has been conducted in the benthos, we also describe data from estuarine water columns. Understanding both the common patterns and the differences between estuaries has important implications for how these critical ecosystems respond to changing environmental conditions.

Keywords Nitrogen · Biogeochemistry · Microbial ecology · Functional gene · Nutrient cycling

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✉ Christopher A. Francis
caf@stanford.edu

[1] Department of Earth System Science, Stanford University, 473 Via Ortega, Stanford, CA 94305-4216, USA

[2] Present address: Department of Marine Sciences, University of Georgia, Marine Sciences Building, Athens, GA 30602-3636, USA

Introduction: Anthropogenic Nitrogen Enrichment of Estuaries

Nitrogen (N) is an important building block for organic molecules such as nucleic acids, amino acids, and pigments and is one of the prime nutrients required for organismal growth. Compared to other nutrients (e.g., carbon and phosphorus), N is particularly important in estuaries and many oceanic regions, where it often limits primary productivity (Vitousek and Howarth 1991; Howarth and Marino 2006; Moore et al. 2013). As a result, influxes of N can lead to massive phytoplankton and algal blooms (Mallin et al. 1991; Beman et al. 2005), which can have harmful ecological effects such as high concentrations of toxic compounds or decomposition-induced hypoxia (Anderson et al. 2002). Globally, the vast majority of N exists as atmospheric dinitrogen gas (N_2), which is unavailable to most organisms. In pre-industrial times, shunting N from this atmospheric reserve into "reactive N" (N_r) and thus into the biosphere depended largely on biological N_2-fixation, with a small additional contribution from abiotic N_2-fixation (Galloway et al. 2004). But in the early twentieth century, development of industrial methods to fix N_2 changed this balance by allowing for synthetic production of nitrogenous fertilizers (Erisman et al. 2008). This practically limitless source of N_r led to spikes in food production and human population, increasing delivery of N to rivers and coastal

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waters from both non-point sources (such as fertilizer runoff) and point sources (such as sewage effluent and urban runoff; Boyer et al. 2006). Additionally, fossil fuel burning leads to substantial emissions and subsequent deposition of gaseous N (Erisman et al. 2008; Fowler et al. 2013). Thus, recent anthropogenic development has profoundly perturbed the planet's N cycle (Steffen et al. 2015).

Coastal nutrient enrichment is one of the most devastating ecological consequences of rapid human population growth and development. The effects of N pollution are particularly acute in estuaries, due to their locations at the mouths of large watersheds or close to dense urban regions (Nixon et al. 1996; Howarth et al. 2012). In fact, the majority of estuaries in the USA are categorized as at least moderately eutrophic (Bricker et al. 2008), suggesting that estuarine eutrophication is a significant environmental problem even in "developed" countries and is likely to worsen with further anthropogenic development and nutrient loading.

N in estuaries is present in numerous forms, including gases, inorganic ions, and organic molecules. The N cycle is predominantly driven by oxidation/reduction reactions catalyzed by microbes that use nitrogenous compounds for energy (Fig. 1). Additional contributions come from N taken into the cell and assimilated into biomass by both autotrophic and heterotrophic microbes, either by fixation of N_2 gas or uptake of dissolved N_r (Fig. 1). Microbial activities drive much of the biogeochemical cycling of N, changing the concentrations of nitrogenous compounds in the environment (Ward 2012). Comprehension of N cycling in any ecosystem, therefore, requires a thorough understanding not only of relevant biogeochemical rates, but also the structure (diversity and abundance) and activity of the microbial communities driving such processes.

Both biogeochemical and microbial studies of estuarine N cycling have proliferated in recent years. The development of relatively inexpensive methods of measuring N cycling rates expanded the number of research labs and commercial facilities capable of analyzing such samples, leading to a wealth of rate measurement data from a variety of estuaries worldwide. At the same time, technological advances in nucleic acid sequencing [e.g., next-generation sequencing (NGS) platforms] have dramatically changed the field of microbial ecology, including a proliferation of data on N cycling microbes in estuaries. Here, we synthesize current knowledge of both the biogeochemistry and microbial ecology of the estuarine N cycle. Our focus is dissimilatory processes and others catalyzed by bacteria and archaea (e.g., remineralization, heterotrophic assimilation, and N_2-fixation); while assimilatory uptake by photosynthetic organisms (phytoplankton and macrophytes) and macrofaunal N excretion can also have distinct impacts on estuarine N cycling, these processes have been reviewed extensively elsewhere (Regnault 1987; Hecky and Kilham 1988; Valiela et al. 1997; Prins et al. 1998; Flindt et al. 1999; Anderson et al. 2002; Newell 2004; Boynton and Kemp 2008; Glibert et al. 2016). For each process, trends in biogeochemical rates will first be described, followed by a discussion of the relevant microbial communities, primarily focused on functional gene analyses. For both types of data, we seek to identify relationships between environmental variables and N cycling processes/microbial communities that are shared across ecosystems and, when possible, relate these correlations to mechanistic hypotheses based on theoretical work or laboratory manipulations.

Heterotrophic Assimilation and Remineralization

Microbial N Uptake

Just as photosynthetic organisms require N for assimilatory purposes, all heterotrophic and chemoautotrophic microbes also take up N to build biomass (assimilatory uptake), while some also take up N_r to fuel energy-conserving reactions (dissimilatory uptake). Therefore, there is direct competition for N_r in estuary waters between photoautotrophic, heterotrophic, and chemoautotrophic microbes. Competition for N_r is mostly for ammonium (NH_4^+) or nitrate (NO_3^-), the most common forms of N_r in estuaries. Prokaryotic ammonium assimilation occurs via two main pathways: a high-affinity ammonium transporter (encoded by *amtB*) moves ammonium into the cell, where it is combined with glutamate to form glutamine by the glutamine synthetase (GS) enzyme; and a low-affinity transport system in which ammonia is passively transported into the cell (e.g., via diffusion) and combined with α-ketoglutarate by the glutamate dehydrogenase enzyme (GDH, encoded by *gdh* genes) to produce glutamate (Merrick and Edwards 1995). While not providing direct phylogenetic information, the ratio of GS/GDH enzyme activity has been used to assess microbial N availability in the ocean (Hoch et al. 2006). Many prokaryotes have multiple copies of *amtB*, often from different phylogenetic clades (Thomas et al. 2000b; McDonald et al. 2012; Offre et al. 2014). Microbial GS genes occur as several different types (GSI, GSII, and GSIII): most prokaryotes have GSI, encoded by *glnA*, while a small number of bacteria have GSIII and eukaryotes typically have GSII (Brown et al. 1994). Finally, there are four major types of GDH, three of which (GDH-1, GDH-2, and GDH-4) are common in prokaryotes, but phylogenetic analysis of *gdh* genes suggests numerous instances of lateral gene transfer across domains (Andersson and Roger 2003). Little is known about the diversity of this suite of N assimilation genes in estuaries or the ocean.

Ammonium is usually preferred to nitrate for assimilatory growth because it is reduced and therefore requires less energy to build amino acids (Eppley et al. 1969; Dortch 1990). Thus, competition for ammonium is thought to be especially fierce. Although heterotrophic microbes can be responsible for

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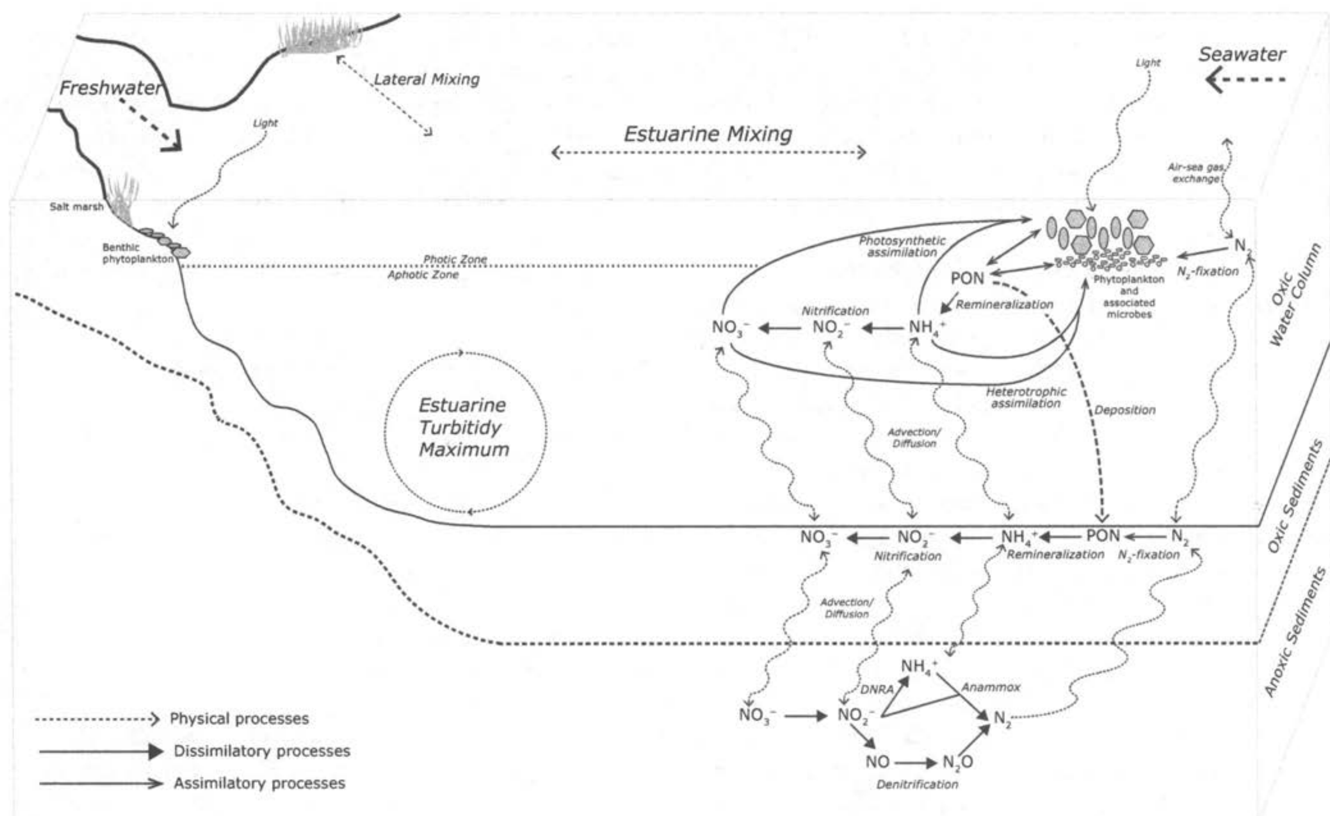

Fig. 1 Diagram of estuarine N cycling processes. Water column processes assume oxic conditions throughout; if anoxia were present in the water column, processes shown in the anoxic sediments would also occur in the water column. Filled arrow heads show dissimilatory processes, while open heads (and solid lines) show assimilatory processes. Dashed lines show physical processes. For simplicity, only N_2 is depicted as diffusing through the water column and into the atmosphere; NO and N_2O diffuse this way as well

significant fractions of ammonium uptake in marine and estuarine waters, their contribution to overall ammonium uptake (i.e., the fraction of total ammonium uptake accounted for by heterotrophs) is highest in oligotrophic waters and lower in more eutrophic waters such as estuaries (Ducklow and Carlson 1992; Kirchman 1994; Hoch and Kirchman 1995; Mulholland et al. 2003; Trottet et al. 2016). This is ascribed to differences in cell size and substrate affinity between phytoplankton and heterotrophic microbes: smaller surface area allows microbes to more efficiently scavenge nutrients when concentrations are low, whereas the large cell volume of phytoplankton allows for rapid nutrient uptake and storage (outcompeting heterotrophs) when supply is plentiful (Cotner and Wetzel 1992; Kirchman 1994). Seasonal data from Long Island Sound also indicated a higher fraction of bacterial ammonium uptake during summer, suggesting that bacteria may outcompete phytoplankton for ammonium when productivity is high and ammonium turnover is rapid (Fuhrman et al. 1988). However, in turbid estuaries where phytoplankton growth is light-limited, bacteria can account for a significant fraction of ammonium uptake even when nutrients are plentiful (Kroer et al. 1994; Middelburg and Nieuwenhuize 2000a, b; Andersson et al. 2006). Measurements of GS activity indicate that this high-affinity ammonium uptake enzyme is highly active in oligotrophic waters, whereas the low-affinity GDH enzyme is more active in eutrophic estuary waters (Jørgensen et al. 1999; Hoch et al. 2008).

Additionally, little is known about heterotrophic nitrate uptake in estuary waters, despite indications that a diverse array of heterotrophs assimilate substantial fractions of available nitrate in some regions of the ocean (Allen et al. 2001, 2002; Fouilland et al. 2007; Bradley et al. 2010). In one of the only studies measuring heterotrophic ammonium and nitrate uptake in an estuary, heterotrophic bacteria were responsible not only for the majority of ammonium uptake in the Thames Estuary, but two-thirds of the nitrate uptake as well, with the majority of heterotrophic N assimilation in the nutrient-rich inner estuary coming from nitrate (Middelburg and Nieuwenhuize 2000a). Additionally, paired light and dark uptake incubations through numerous turbid European estuaries suggested both phytoplankton and bacteria played a role in ammonium and nitrate uptake (Middelburg and Nieuwenhuize 2000b). Another study comparing bacterial N uptake across a range of aquatic ecosystems found nitrate uptake in marine waters but nitrate release in estuaries (Kroer et al. 1994), suggesting that heterotrophic nitrate uptake in estuaries may not be universal.

Despite evidence that heterotrophic activity accounts for a significant fraction of ammonium or nitrate uptake in some estuaries, little is known about the diversity or activity of prokaryotic

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nitrogen uptake genes in these environments. While metatranscriptomes from numerous estuaries and coastal plumes have shown that *amt* genes from heterotrophic and ammonia-oxidizing microbes can be highly expressed in these waters (Gifford et al. 2011; Hollibaugh et al. 2011; Hewson et al. 2014; Hollibaugh et al. 2014; Satinsky et al. 2014), these studies only reported the abundance of all *amt* transcripts in their libraries and did not investigate the taxonomic breakdown of these transcripts, though Hollibaugh et al. (2011, 2014) noted the high expression of *amt* transcripts from *Thaumarchaeota*. Indeed, few studies have investigated the diversity or expression of genes from nitrogen assimilatory pathways in the field. Evidence from ^{15}N stable isotope probing (SIP) experiments in coastal Florida and California surface waters have suggested marine *Gamma*- and *Alphaproteobacteria*, as well as Marine Group II Euryarchaeota, actively take up nitrate (Morando and Capone 2016; Wawrik et al. 2012). In San Francisco Bay waters, data obtained by Chip-SIP (in which SIP is combined with microarray hybridization and isotopic enrichment is detected using nanoscale secondary ion mass spectrometry) showed that a diverse range of common estuarine bacteria, including *Roseobacter* (*Alphaproteobacteria*), OM43 (*Betaproteobacteria*), and *Bacteriodetes*, can rapidly assimilate ammonium (Mayali et al. 2013). While data on the diversity of assimilatory nitrate reductase (*nasA*) genes has been collected from a small number of marine regions (e.g., Allen et al. 2001), little is understood about *nasA* in estuaries or coastal environments. Clearly, much is still to be learned about the microbial communities underpinning DIN uptake in estuaries.

In addition to DIN uptake, bacterial assimilation can also account for a high fraction of dissolved organic N (DON) uptake in estuaries and coastal waters (Seitzinger and Sanders 1997; Middelburg and Nieuwenhuize 2000a; Veuger et al. 2004). DON in estuaries is a complex blend of labile and recalcitrant molecules, including amino acids, urea, protein, and humic substances (among others), with turnover times ranging from hours to days for individual compounds (Berman and Bronk 2003). Much of the DON pool is metabolized by estuary microbes, including urea (Lomas et al. 2002; Mulholland et al. 2003; Twomey et al. 2005; Andersson et al. 2006; Jørgensen 2006), amino acids (Crawford et al. 1974; Coffin 1989; Fuhrman 1990; Tupas and Koike 1991; Kroer et al. 1994; Hoch and Kirchman 1995; Middelburg and Nieuwenhuize 2000a; Mulholland et al. 2003; Andersson et al. 2006; Jørgensen and Middelboe 2006), and polyamines (Höfle 1984; Liu et al. 2015; Mou et al. 2015). Heterotrophic bacteria appear capable of using this sporadically plentiful N source in productive waters, with molecular evidence suggesting that a wide range of heterotrophs express transporter genes and rapidly respond to DON availability (Mou et al. 2010; Poretsky et al. 2010; Mou et al. 2011; Lu et al. 2015), but studies targeting differential responses or niche partitioning related to microbial organic N uptake are rare. Two studies in San Francisco Bay found a diverse suite of bacteria assimilating N from amino acids, including Marine Group A, numerous *Alphaproteobacteria* (*Roseobacter* and *Rhodobacteriaceae*), and *Planctomycetes* (Mayali et al. 2013, 2014), indicating that numerous heterotrophic microbes can use DON as a N source.

N Remineralization

Nutrient recycling rates in estuaries are high, and labile organic N is often rapidly remineralized to ammonium. Unlike the open ocean, where the majority of organic matter (OM) decomposition occurs in the water column, a high fraction of OM produced in estuaries is decomposed in sediments; since the photic zone of the water column is physically close to the benthos, OM is rapidly transported to the sediments while still relatively labile (Nixon 1981). Consequently, most benthic N remineralization rates in the literature are estimated by measuring ammonium effluxes from sediments over time (Boynton and Kemp 2008), but these measurements can be biased in either direction: dissimilatory nitrate reduction to ammonium (DNRA) can directly produce significant amounts of ammonium in some estuaries (e.g., Gardner et al. 2006; see DNRA section below), leading to an additional source of ammonium; alternatively, remineralized ammonium can be rapidly assimilated or nitrified (and potentially lost due to coupled nitrification-denitrification), consuming a significant fraction of ammonium before it can diffuse into the water (Tobias et al. 2003; Lin et al. 2011). For these reasons, bulk ammonium fluxes may not always represent an accurate estimate of N remineralization itself. Yet, because measurements using ^{15}N tracers (i.e., production of $^{15}NH_4^+$ following incubation with ^{15}N-labeled organic N or monitoring "dilution" of an amended $^{15}NH_4^+$ pool) are rare, ammonium flux measurements remain the predominant method used to estimate remineralization rates.

In his early review of nutrient remineralization in coastal ecosystems, Nixon (1981) emphasized the importance of regenerated N in supporting primary productivity, as ammonium diffusing from the sediments can, in many estuaries, be rapidly transported to the photic zone and assimilated by phytoplankton. Recent studies have corroborated the idea that benthic ammonium can supply a large fraction of photosynthetic N demand (Pratihary et al. 2009; York et al. 2010; Bernard et al. 2014), though phytoplankton nutritional demand exceeds benthic N fluxes in some estuaries, as well (Murrell et al. 2009; Mortazavi et al. 2012). Additionally, Nixon (1981) described the importance of productivity and benthic-pelagic coupling in many estuaries, with OM deposition leading to high rates of both benthic respiration and ammonium efflux (Nixon 1981). Boynton and Kemp (2008) provided a thorough synthesis of benthic-pelagic ammonium flux measurements in estuaries, which ranged from relatively low ammonium influxes (< 0.1 mmol m^{-2} h^{-1}) to effluxes of nearly 3 mmol m^{-2} h^{-1}. Generally, ammonium effluxes were higher in marine and brackish regions compared to freshwater estuarine regions, likely due to their greater overall

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phytoplankton productivity (and therefore greater labile OM deposition). Effluxes were often high in shallow estuaries, though benthic photosynthesis in shallow systems can also temper N effluxes. Sedimentation rates of labile OM appeared to be important in driving ammonium production, with temperature also playing an important (and mechanistically related) role in many ecosystems (Boynton and Kemp 2008).

Many recent studies reinforce that benthic N remineralization is often correlated to either temperature (Gardner and McCarthy 2009; Giblin et al. 2010; Mortazavi et al. 2012; Bernard et al. 2014; Roberts and Doty 2015) or OM availability (Fulweiler and Nixon 2009; Nixon et al. 2009; Pratihary et al. 2009; Mortazavi et al. 2012; McManus et al. 2014; Pérez-Villalona et al. 2015), with highest ammonium effluxes occurring during summer months, often following phytoplankton blooms. Because OM deposition often stimulates benthic respiration, correlations between sediment oxygen demand and ammonium efflux are also common (Foster and Fulweiler 2014; Tucker et al. 2014), though ammonium production has also been found in regions with low respiration (Smith and Caffrey 2009). Benthic macrofaunal activity can stimulate ammonium efflux rates, either through direct excretion or by stimulating microbial decomposition (D'Andrea and DeWitt 2009; Kellogg et al. 2013; Murphy et al. 2016). Finally, ammonium effluxes are often correlated with salinity along an estuary, though not always in a consistent manner (Fulweiler et al. 2010; Giblin et al. 2010; Weston et al. 2010; York et al. 2010). These patterns may be related to regional differences in nutrient loading or productivity (e.g., Fulweiler et al. 2010) and are complicated by inorganic desorption of porewater ammonium, which can lead to significant abiotic fluxes of ammonium where fresh and brackish waters meet (Weston et al. 2010).

In contrast to the abundance of benthic data, relatively few measurements of water column remineralization have been made in estuaries. Bronk and Steinberg (2008) reviewed pelagic remineralization measurements from marine areas, including estuaries and coastal waters. In these productive regions, remineralization rates were often related to temperature, productivity (i.e., OM availability), or salinity. To further complicate matters, ammonium production can be related either to zooplankton grazing or microbial activity (Bronk and Steinberg 2008), and field measurements of DON remineralization are complicated by simultaneous remineralization and assimilation (Tupas and Koike 1991). However, in some productive estuaries, pelagic N remineralization can convert a substantial fraction of organic N to ammonium prior to benthic deposition (Hollibaugh 1978; Hollibaugh et al. 1980; Bourgoin and Tremblay 2010; Ferguson and Eyre 2010; Bronk et al. 2014), particularly when OM is N-rich (e.g., amino acids or marine detritus; Bourgoin and Tremblay 2010). Understanding the relative contributions of pelagic N remineralization in estuaries is clearly an area where further study is needed.

Another method commonly used to estimate rates of microbial remineralization is measuring activities of ectoenzymes (i.e., enzymes located at the cell surface or outside the cell): substrates with fluorogenic moieties are added to a sample and fluorescence is measured over time, as cleavage of substrate bonds releases the fluorogenic molecule (Hoppe 1983). Of particular interest for N remineralization is aminopeptidase, an ectoenzyme that cleaves amino groups from peptides. In estuary waters, aminopeptidase activity (APA) is often correlated with heterotrophic bacterial production or microbial abundance, with highest peptide hydrolysis rates in summer and often in productive mid-estuary regions (Unanue et al. 1993; Murrell et al. 1999; Cunha et al. 2000; Patel et al. 2000; Karrasch et al. 2003; Murrell 2003; Taylor et al. 2003; Santos et al. 2009). Coupling between APA and bacterial production suggests that DON remineralization via ectoenzymes is highest when labile OM is readily available (e.g., Murrell et al. 1999). Interestingly, a mesocosm study showed that a large amount of humic-rich terrestrial DON was hydrolyzed upon transport to marine waters, possibly due to effects of pH or ions on enzyme activity (Stepanauskas et al. 1999). APA in some estuaries is highest in oligotrophic waters, with DIN limitation necessitating the use of DON (Mulholland et al. 2003; Taylor et al. 2003; Cunha and Almeida 2009), while in others, highest activity is in eutrophic regions, presumably due to high substrate availability and fluxes (Hoppe et al. 1988; Cunha and Almeida 2009). In many estuaries, a high fraction of APA is found in the < 0.2 μm fraction, indicating substantial rates of peptide hydrolysis by extracellular enzymes (Unanue et al. 1993; Karrasch et al. 2003), though in some systems, more activity is associated with larger particles (Mulholland et al. 2003).

In addition to the water column, a few studies have measured APA in estuary sediments. In a salt marsh adjacent to Long Island Sound, benthic APA was highest in spring and summer, and longer peptides (containing more than two amino acids) were hydrolyzed faster than dipeptides or leucine (Pantoja and Lee 1999). Shifts in APA were documented in sediments experimentally transplanted along an estuary gradient, concomitant with changes in overall microbial diversity (though the relationship between APA and individual microbial clades remains unknown; Reed and Martiny 2013). While studies indicate high rates of N remineralization via ectoenzymes can occur in surface sediments, little is known about the relative contribution of APA in sediments versus the water column to total N remineralization in estuaries.

Nitrogen Fixation

N_2-Fixation Rates in Estuaries: Important Inputs Even to Eutrophic Systems?

Because the atmosphere is nearly 80% N_2, N limitation of most ecosystems on Earth initially is counterintuitive, but the strength of the triple bond in this molecule renders it inert to the majority of

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microbes. To exploit this massive store of N, a diverse group of microbes can "fix" N_2 into ammonium via the nitrogenase enzyme (Berman-Frank et al. 2003). The energetic load required to fix N_2 is reflected in the intense requirement of 16 ATP needed to fix one molecule of N_2; for this reason, while N_2-fixation allows some microbes to access a practically unending N supply, this advantage comes at a significant energetic cost. Yet, N_2-fixation is a clear advantage in environments such as oligotrophic ocean gyres, where N_r is scarce (Karl et al. 1997; Capone et al. 2005; Casciotti et al. 2008).

Due to this energetic demand, N_2-fixation is often assumed to only be relevant in extremely oligotrophic environments or patchy environments where biological N demand is high (e.g., the soil rhizosphere or microbial mats). Therefore, the contribution of N_2-fixation to N loading in estuaries and other N_r-replete ecosystems was traditionally thought to be minimal, even in cases when N appeared to limit primary productivity (Howarth et al. 1988). While it was long-known that heterotrophic bacteria were also capable of N_2-fixation in estuary sediments (Herbert 1975) and salt marshes (Jones 1974; Capone and Carpenter 1982), the ecological importance of these processes in estuaries was assumed to be low. Renewed interest in benthic N_2-fixation has come from recent work measuring N_2 fluxes and conversion of $^{15}N_2$ to ^{15}N-labeled organic N in whole-core incubations (Table 1), confirming that heterotrophic estuary sediments can be significant sources of N_r due to N_2-fixation (Gardner et al. 2006; Fulweiler et al. 2007; Foster and Fulweiler 2014; Newell et al. 2016b). OM quality and quantity appear to affect rates of benthic N_2-fixation, suggesting complex interactions between N_2-fixation and denitrification, with net N_2-fixation favored when OM quantity or quality are low (Fulweiler et al. 2013; Andersson et al. 2014). Additionally, using stable isotope rate incubations to measure N_2-fixation ($^{15}N_2$ conversion to particulate organic N) has suggested that some estuary waters have N_2-fixation rates surpassing most regions of the ocean, due to a combination of heterotrophic and cyanobacterial activity (Bentzon-Tilia et al. 2015). In all, these studies paradoxically suggest that N_2-fixation may be an important source of N_r in many estuaries. While the paradigm of N_2-fixation only being an important process in N-limited aquatic ecosystems may be shifting, significant work remains to determine the environmental controls on N_2-fixation rates in estuaries and coastal environments.

Diversity and Activity of N_2-Fixing Microbes in Estuaries

Molecular analyses of N_2-fixing microorganisms have largely focused on the *nifH* gene, which codes for component II of the nitrogenase enzyme (Zehr and McReynolds 1989; Zehr et al. 2003). Environmental *nifH* sequences largely group into four major clusters, designated clusters I–IV (Chien and Zinder 1996; Zehr et al. 2003). While N_2-fixing cyanobacteria are common in both eutrophic and oligotrophic freshwater systems (e.g., McCarthy et al. 2007; Carey et al. 2008), the prevalence of cyanobacterial *nifH* genes varies between estuaries, and a diverse suite of presumably heterotrophic and anaerobic bacterial *nifH* genes is common in many estuaries (Zehr et al. 2003; Riemann et al. 2010). For example, cyanobacterial genes were common in surface waters of the Neuse Estuary but rare in Chesapeake Bay, and the majority of *nifH* genes present in the waters of both estuaries were cluster I sequences from *Alpha-*, *Beta-*, and *Gammaproteobacteria* (Affourtit et al. 2001; Jenkins et al. 2004; Moisander et al. 2007). In addition to these water column studies, diverse *nifH* sequences are also present in estuary sediments, with benthic communities commonly including cluster I *Proteobacteria* and cluster III sequences including common anaerobic bacteria (Burns et al. 2002; Moisander et al. 2007; Fulweiler et al. 2013; Brown and Jenkins 2014; Newell et al. 2016a).

The high *nifH* diversity in many environments makes this gene an ideal target for NGS applications (Farnelid et al. 2011). In Danish coastal estuary waters, high-throughput *nifH* sequencing revealed thousands of OTUs but suggested only a small fraction accounted for the majority of reads (Bentzon-Tilia et al. 2015; Severin et al. 2015), with heterotrophic diazotrophs (e.g., proteobacterial cluster III) abundant in eutrophic waters (likely due to sediment resuspension) and cluster I cyanobacteria more abundant in lower-nutrient waters (Bentzon-Tilia et al. 2015). The same studies also found that the diversity of *nifH* genes and mRNA transcripts were profoundly different and highly variable when measured in the environment through time or in response to nutrient additions. Cluster I and cluster III sequences were also the dominant *nifH* sequences in the Baltic Sea: although oxic and anoxic waters contained both clusters, cluster I sequences (cyanobacterial and proteobacterial) were common in oxic waters whereas cluster III sequences from anaerobes were common in anoxic waters (Farnelid et al. 2013). In Spencer Gulf, a nutrient-rich inverse estuary in Australia, *nifH* amplicon sequencing revealed UCYN-A cyanobacteria as the dominant diazotrophs, though UCYN-A ecotypes (and overall diazotrophic diversity) showed clear shifts related to salinity and nutrient concentration (Messer et al. 2015). Overall, studies of *nifH* in estuaries suggest a complex picture of highly diverse communities and complicated relationships between environmental drivers and gene diversity, abundance, and expression, with no clear patterns driving *nifH* diversity between ecosystems (Moisander et al. 2007; Severin et al. 2015). Understanding how environmental factors affect the diversity, abundance, and activity of the wide variety of microbial groups capable of N_2-fixation is crucial for understanding their contributions to estuarine N biogeochemistry.

Nitrogen Loss: Denitrification and Anammox

Denitrification Rates

Because of the longstanding knowledge that excess N_r can lead to adverse ecological effects, significant effort has

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Table 1 Common functional gene markers and rate methods for N-cycling processes

	Functional genes		Common rate methods	
N_2 Fixation	*nifHDK* (Nitrogenase)	Zehr and McReynolds 1989	Acetylene reduction	Stewart et al. 1967
			N_2:Ar (MIMS)	Kana et al. 1994
			$^{15}N_2$ tracer	Neess et al. 1962; Montoya et al. 1996
			$^{15}NO_3^-$ tracer (isotope pairing)	An et al. 2001
Nitrification	*amoA* (Ammonia monooxygenase)	Rotthauwe et al. 1997; Francis et al. 2005	^{14}C tracer + inhibitor	Somville 1978
	nxrAB (Nitrite oxidoreductase)	Poly et al. 2008; Pester et al. 2014	NH_4^+ flux + inhibitor	Henriksen 1980
			$^{15}NH_4^+$ or $^{15}NO_2^-$ tracer	Miyazaki et al. 1973; Olson 1981
			$^{15}NO_3^-$ dilution	Koike and Hattori 1978b
			Amended sediment slurries	Hansen et al. 1981
Denitrification	*narG*, *napA* (Nitrate reductase)	Flanagan et al. 1999; Gregory et al. 2000	N_2O production + acetylene ("acetylene inhibition")	Sørensen 1978b
	nirS, *nirK* (Nitrite reductase)	Smith and Tiedje 1992; Braker et al. 1998	^{15}N isotope tracers/pairing	Nielsen 1992
	norB (Nitric oxide reductase)	Braker and Tiedje 2003	N_2:Ar (MIMS)	Kana et al. 1994
	nosZ (Nitrous oxide reductase)	Scala and Kerkhof 1998	N_2 fluxes	Seitzinger et al. 1980
Anammox	*Scalindua*-like *nirS* (Nitrite reductase)	Lam et al. 2009	^{15}N amended sediment slurries/water (potential rates)	Thamdrup and Dalsgaard 2002; Kuypers et al. 2003
	hzoAB (Hydrazine oxidoreductase)	Schmid et al. 2008	Revised isotope pairing technique	Risgaard-Petersen et al. 2003; Trimmer et al. 2006
	hzsAB (Hydrazine synthase)	Harhangi et al. 2012; Wang et al. 2012b		
DNRA	*nrfA* (Nitrite reductase)	Mohan et al. 2004	$^{15}NO_3^-$ tracer	Koike and Hattori 1978a
Assimilation	*amtB* (Ammonia transporter)	Thomas et al. 2000a	^{15}N tracers + eukaryotic/prokaryotic inhibitors	Wheeler and Kirchman 1986
	glnA (Glutamine synthetase)	Kramer et al. 1996	^{15}N tracers + size fractionation of water	Kirchman et al. 1989
	nasA (Assimilatory nitrate reductase)	Allen et al. 2001		

Modified and updated from Zehr and Ward (2002) and Santoro (2010)

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focused on studying N_r loss processes in estuaries. Until recently, denitrification was the sole process known to convert N_r to N_2 and thus lead to degassing of N. Denitrification is a respiratory metabolic process in which microbes use nitrate as a terminal electron acceptor in the absence of oxygen. In the canonical denitrification pathway, nitrate is respired to nitrite, followed by stepwise reductions to nitric oxide (NO), nitrous oxide (N_2O), and finally N_2 (Zumft 1997). Nitrate can be supplied as an external source (e.g., diffusing into sediments) or by in situ nitrification, referred to as "direct denitrification" and "coupled nitrification-denitrification," respectively. Although the majority of anaerobic nitrate reduction produces N_2, some N_2O also "leaks" out during denitrification. Because of its enormous potency as a greenhouse gas, N_2O produced via denitrification has garnered much attention and is thought to have a substantial impact on the global N_2O budget (Anderson and Levine 1986; Seitzinger and Kroeze 1998; Codispoti 2010; Bianchi et al. 2012).

Due to a lower thermodynamic yield of respiring nitrate compared to oxygen, denitrification is typically restricted to suboxic or anoxic environments, though there is some evidence of active denitrification occurring in aerobic conditions as well (Robertson and Kuenen 1984; Lloyd et al. 1987). While denitrification can occur in the water column of stratified anoxic estuaries (Crump et al. 2007; Manning et al. 2010; Hietanen et al. 2012), many estuaries are well-ventilated and therefore oxic, with denitrification consequently relegated to the sediments. Measuring in situ denitrification rates in sediments is notoriously difficult; among the numerous common methods are measuring N_2O production in the presence of acetylene ("acetylene block"), measuring $\delta^{15}N_2$ following ^{15}N tracer additions, and measuring N_2/Ar gas ratios via membrane inlet mass spectrometry (MIMS; Table 1; Seitzinger et al. 1993; Cornwell et al. 1999; Eyre et al. 2002). Using stable isotope tracers has the advantage of distinguishing between direct denitrification and coupled nitrification-denitrification (Nielsen 1992). While the range of estuarine denitrification is quite large, data synthesized by Joye and Anderson (2008) showed that rates in most estuaries are approximately 0.1 to 10 mmol m^{-2} day^{-1}, with high rates often measured in shallow eutrophic systems (Joye and Anderson 2008).

Denitrification rates often vary with salinity, with highest N loss in brackish and freshwater regions compared to marine regions (Rysgaard et al. 1999; Fear et al. 2005; Dong et al. 2009; Giblin et al. 2010; Francis et al. 2013). Since salinity covaries with other variables in most estuaries (e.g., nitrate, productivity, and dissolved oxygen), correlations between denitrification rates and salinity may be due to a multitude of drivers. Bottom water nitrate concentrations (which can be high at the head of many estuaries due to external inputs) can drive high direct benthic denitrification if nitrate diffuses into the sediments and is then respired, as is common in eutrophic systems with very high nitrate loadings (Rysgaard et al. 1999; Dong et al. 2000; Tobias et al. 2003; Deek et al. 2013; Bernard et al. 2014; Cornwell et al. 2014). However, denitrification can also depend on bottom water oxygen concentrations, largely due to effects on benthic nitrification and thus coupled nitrification-denitrification (Seitzinger 1988; Rysgaard et al. 1994). When oxygen is depleted, denitrification rates plummet due to a slowing of aerobic nitrification and thus coupled nitrification-denitrification (Jenkins and Kemp 1984; Kemp et al. 1990; Caffrey et al. 2003; Jäntti et al. 2011; Cornwell et al. 2015). On the other hand, benthic oxygen production via photosynthesis can stimulate coupled nitrification-denitrification (Rysgaard et al. 1995; An and Joye 2001; Gao et al. 2012), though if ammonium or nitrate are scarce, benthic primary productivity may inhibit nitrification or denitrification due to direct competition for these substrates (Rysgaard et al. 1995; Risgaard-Petersen 2003). Similarly, numerous studies have found increased rates of denitrification in sediments with active macrofaunal or plant communities. Activity of these organisms can ventilate the upper benthic layers with oxygen and nitrate (if the bottom waters are nitrate-rich) and therefore stimulates nitrification and denitrification, respectively; animal shells can also provide a solid substrate for the growth of microbial biofilms, stimulating biogeochemical activity (Binnerup et al. 1992; Rysgaard et al. 1995; Barnes and Owens 1999; Nizzoli et al. 2007; Kellogg et al. 2013; Alldred and Baines 2016; Humphries et al. 2016; Moulton et al. 2016).

Denitrification rates can be highly correlated with organic C content of sediments or sediment oxygen demand (a measure of the overall oxygen uptake by sediments and thus heterotrophic activity; Seitzinger and Giblin 1996; Barnes and Owens 1999; Fear et al. 2005; Piehler and Smyth 2011; Cornwell et al. 2014, 2015), as high heterotrophic oxygen consumption is often driven by high inputs of OM, which can also fuel denitrification once oxygen is (rapidly) depleted. At the ecosystem scale, denitrification (as estimated by N budgets) appears to be strongly correlated with water residence time (Nixon et al. 1996; Howarth et al. 2012), suggesting that enhanced nutrient processing occurs in riverine and estuarine systems with lower flow.

In estuaries with hypoxic or anoxic waters, measurements of denitrification rates in the water column are surprisingly scarce, perhaps due to the assumption that rapid benthic nitrate consumption would lead to nitrate limitation of pelagic denitrification. Measurements of nitrate natural abundance stable isotopes or time courses of N_2 accumulation suggest that a substantial fraction of total denitrification in these estuaries may occur in the water column, though partitioning the processes between sediments and water remains challenging (Kana et al. 2006; Manning et al. 2010; Bourbonnais et al. 2013). Thus, understanding the contribution of water column denitrification to N_r loss in anoxic estuary waters is an area where further research is needed.

Microbial Ecology of Denitrifiers

The majority of known denitrifiers are heterotrophic bacteria that couple organic carbon oxidation to the stepwise anaerobic

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reduction of nitrate to N_2 gas. Denitrification is widespread across a diverse array of taxa (Coyne et al. 1989; Heylen et al. 2006; Wallenstein et al. 2006; Graf et al. 2014), and many denitrifiers are also capable of respiring oxygen (Robertson and Kuenen 1984), complicating the use of 16S rRNA genes to definitively identify denitrifiers within mixed microbial communities. Genes involved in the canonical denitrification pathway (and the corresponding encoded enzymes) are *nar* (membrane-bound nitrate reductase) or *nap* (periplasmic nitrate reductase), *nir* (dissimilatory nitrite reductase), *nor* (nitric oxide reductase), and *nos* (nitrous oxide reductase), though there are many denitrifiers that only possess partial pathways with some genes missing (Zumft 1997). Any of these genes can theoretically be used as a functional marker for denitrification (Table 1); however, some bacteria respiring nitrate to ammonium also use Nar (although most DNRA bacteria appear to use Nap; Richardson et al. 2001; Kraft et al. 2011). While most denitrifiers appear to use Nar for nitrate reduction, some exclusively use Nap (Kraft et al. 2011). Because nitrite reduction to nitric oxide is the first committed step of the pathway to a gaseous product (whereas nitrite produced by nitrate reduction could also be reduced to ammonium or assimilated), *nir* genes have become the most widely used markers for denitrifiers (Smith and Tiedje 1992; Braker et al. 1998; Mosier and Francis 2010).

In denitrifiers, *nir* genes have two distinct varieties, *nirS* (encoding iron-rich cytochrome-cd_1) and *nirK* (encoding a copper-containing enzyme), with most denitrifying bacteria containing one of the two but not both (Coyne et al. 1989); while recent genomic analyses have suggested that a small number of bacteria have both *nirS* and *nirK* (Graf et al. 2014), their functionality has yet to be confirmed. The taxonomic diversity of *nirK*-type denitrifiers is greater than that of *nirS*, likely due to horizontal gene transfer. Thus, while *nirS* diversity is somewhat reflective of 16S diversity, *nirK* is not (Heylen et al. 2006; Graf et al. 2014). Additionally, a recent genomic analysis suggested that a high number of *nirK*-encoding bacteria have pathways for both denitrification and DNRA (Helen et al. 2016). Among well-characterized denitrifiers, those with *nirS* were more likely to have a complete denitrification pathway (including *nor* and *nos* genes), suggesting that *nirS*-containing denitrifiers may be more likely to completely reduce nitrite to N_2 (Graf et al. 2014).

In general, *nirS* genes are both more abundant and more diverse than *nirK* in estuary sediments, although this pattern sometimes shifts in different estuarine regions (Nogales et al. 2002; Santoro et al. 2006; Abell et al. 2010; Mosier and Francis 2010; Magalhães et al. 2011; Beman 2014; Smith et al. 2015b; Lee and Francis 2017). Despite the relatively high number of denitrifiers in pure culture, studies of estuary sediments suggest that the most dominant ecotypes in the natural environment are unrelated to any of these strains (Nogales et al. 2002; Santoro et al. 2006; Francis et al. 2013; Lee and Francis 2017). Commonly, a small number of "core" ecotypes account for the majority of *nirS* genes, whether using clone libraries (Dang et al. 2009; Francis et al. 2013), microarrays (Bulow et al. 2008; Bowen et al. 2011), or high-throughput sequencing (Bowen et al. 2013; Lee 2015; Saarenheimo et al. 2015), although overall genetic diversity in these studies was typically high and individual sites or regions often have many endemic ecotypes as well. Denitrifier diversity often varies along the estuarine salinity gradient, with distinct communities in fresh/brackish and marine regions (Nogales et al. 2002; Abell et al. 2013; Francis et al. 2013; Lee and Francis 2017). In addition, recent redesigning of PCR primers suggested that *nir* gene diversity in soils may be even higher than previously suspected (Wei et al. 2015), though these primers have yet to be tested in estuaries.

Because denitrification is often active only in estuary sediments, fewer studies have documented the abundance or diversity of *nir* genes in estuary waters. In ecosystems where seasonal anoxia or hypoxia occur, *nirS* genes have been found in high abundance, particularly at oxic-anoxic interfaces or during the onset of hypoxia; as in estuary sediments, *nir* genes in estuary waters are quite diverse (Hannig et al. 2006; Falk et al. 2007; Zhang et al. 2014). Recent analyses of active microbial communities in seasonally anoxic Chesapeake Bay waters found a high abundance of denitrifier transcripts, particularly at the onset of hypoxia (Hewson et al. 2014; Eggleston et al. 2015), adding to previous evidence of abundant *nirS* genes in similar waters (Hong et al. 2014). Measurements of microbial respiration and nitrate depletion through time confirmed the impact of these microbes on biogeochemical cycling in the Chesapeake (Crump et al. 2007; Lee et al. 2015). In addition to low-oxygen waters, studies of aerobic estuary waters have successfully amplified *nirS* (Hannig et al. 2006; Hong et al. 2014; Zhang et al. 2014), and the complete denitrification pathway was recently found in metagenomes from the water column of the oxic Columbia River Estuary (Fortunato and Crump 2015). Compared to free-living communities, particle-associated microbial communities in oxic estuary waters are often rich in denitrification genes (Smith et al. 2010; Zhang et al. 2014; Fortunato and Crump 2015), suggesting that there may be anoxic microzones on particles allowing for denitrification. However, since many of the microbes containing *nir* genes are also capable of aerobic respiration, the presence of these genes is not necessarily indicative of in situ denitrification.

While heterotrophic denitrifiers coupling nitrate respiration to organic carbon oxidation have been well studied for decades (Payne 1973), more recent discoveries have demonstrated the environmental importance of denitrifiers that use reduced sulfur or iron species as an electron donor (e.g., Dannenberg et al. 1992; Straub et al. 1996). While effects on N cycling between heterotrophic and sulfur- or iron-oxidizing

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denitrifiers are similar, many of the latter are autotrophic (Brettar et al. 2006; Walsh et al. 2009) and thus play a completely different role in the carbon cycle. Although autotrophic denitrifiers were first isolated over a century ago (Beijerinck 1904), demonstrations of their activity in marine or estuarine environments was not demonstrated until decades later (Brettar and Rheinheimer 1991). Sulfur-oxidizing (chemolithoautotrophic) denitrification is a particularly important process at the pelagic redox transition zones of stratified brackish water columns (Labrenz et al. 2005; Crump et al. 2007; Glaubitz et al. 2010; Hawley et al. 2014). In the stratified Baltic Sea, both heterotrophic and autotrophic denitrification occur simultaneously, though OM is typically the predominant energy source (Bonaglia et al. 2016). Microorganisms responsible for sulfur-oxidizing lithotrophic denitrification are typically either SUP05/Arctic96BD-19 group *Gammaproteobacteria* (Bano and Hollibaugh 2002; Sunamura et al. 2004) or *Epsilonproteobacteria* such as *Sulfurimonas* spp. (Grote et al. 2008). However, while the importance of autotrophic denitrifiers in the water column of some estuarine systems has been demonstrated, little is known about the role of sulfur-oxidizing denitrifiers in estuary sediments, due in part to the common assumption that benthic denitrification is fueled only by OM oxidation.

Anammox: The Impact of Anaerobic Ammonium Oxidation on Estuary Biogeochemistry

In the last few decades, our understanding of N loss from aquatic ecosystems has been complicated by the discovery of anaerobic ammonium oxidation ("anammox"), in which NH_4^+ and nitrite (NO_2^-) are combined into N_2 (Fig. 1). This metabolism was hypothesized for decades (Broda 1977) prior to its discovery in wastewater treatment reactors (Mulder et al. 1995); shortly thereafter, anammox was shown to be the metabolism of novel strains of *Planctomycetes* (Strous et al. 1999). Though initially discovered in engineered systems, anammox has since been shown to account for a substantial fraction of N loss from many natural ecosystems, including marine oxygen minimum zones (OMZs), stratified lakes, and marine and estuarine sediments (Francis et al. 2007; Lam and Kuypers 2011). Early documentation of the importance of anammox in marine and sedimentary systems included continental shelf sediments (Thamdrup and Dalsgaard 2002), estuary sediments (Trimmer et al. 2003), anoxic waters in a coastal bay (Dalsgaard et al. 2003), and coastal OMZ waters (Kuypers et al. 2005). The discovery of anammox appeared to solve a decades-old issue in marine OMZs, where a lack of ammonium accumulation occurred despite high rates of anoxic remineralization (e.g., Cline and Richards 1972; Codispoti and Christensen 1985): although aerobic ammonia oxidation could not occur in anoxic waters, anammox (an anaerobic process) could be responsible for this ammonium deficit.

These discoveries led to a debate on the importance of denitrification and anammox for N loss in natural ecosystems, and to myriad of investigations into the environmental drivers of each process. Due to the different N substrates required for each process, anammox is dependent on a supply of both ammonium and nitrite, while denitrification only requires nitrate. One early hypothesis suggested that the percent anammox in a system should be a function of ammonium availability, with injections of ammonium into anoxic environments (assumed to be due to remineralization) increasing the percent anammox (Dalsgaard et al. 2003). Another important difference between anammox bacteria and denitrifiers is their carbon metabolism: anammox bacteria are autotrophs, while most marine and estuarine denitrifiers are heterotrophic (with the exception of some systems dominated by chemoautotrophic denitrification, as described above). Thus, while denitrification depends on the supply of nitrate and organic carbon, anammox rates are uncoupled from OM fluxes as a carbon source. Along these lines, a second hypothesis regarding denitrification and anammox suggested differences in organic carbon requirements drive a relationship where percent anammox is inversely related to OM availability, as denitrification is thermodynamically favorable when OM is abundant and would thus outcompete anammox (Thamdrup and Dalsgaard 2002).

A third hypothesis regarding differences in anammox and denitrification rates focuses on the relative stoichiometry of available carbon and N_r (Koeve and Kähler 2010; Babbin and Ward 2013). In marine OMZs, allochthonous nutrient inputs are relatively low, and the ammonium needed for anammox is therefore provided by remineralization of OM. In these waters, remineralization is largely driven by heterotrophic denitrification; thus, anammox is directly proportional to rates of denitrification, and rates of both are dependent on OM stoichiometry as the ultimate source of carbon for denitrification and ammonium for anammox (Koeve and Kähler 2010). This hypothesis was tested in OM-amended mesocosms of Chesapeake Bay sediments and OMZ waters from the Eastern Tropical North Pacific, and percent anammox in both systems matched theoretical calculations based on OM stoichiometry, with N-rich OM leading to a greater percent anammox (Babbin and Ward 2013; Babbin et al. 2014). Estuaries are complex environments to test these hypotheses, with sediments rich in both OM and ammonium, due to high productivity (followed by OM deposition) and upward flux of remineralized ammonium from anoxic porewaters, respectively (Jørgensen et al. 1990; Grenz et al. 2000; Canuel and Hardison 2016), as well as allochthonous sources of OM and nutrients from terrestrial watersheds, marshes, or anthropogenic inputs (Boschker et al. 1999; McCallister et al. 2004; McIntosh et al. 2015). While direct field tests using in situ estuarine anammox rates are still relatively rare, there have now been enough rate measurements in estuaries to assess

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general patterns. In most estuaries, denitrification appears to drive the bulk of N_2 production. Initial studies found very low percent anammox (the percentage of total N_2 production due to anammox) values (< 10%) in estuary sediments (Thamdrup and Dalsgaard 2002; Trimmer et al. 2003; Risgaard-Petersen et al. 2004b), compared to higher percentages reported from offshore marine sediments (Thamdrup and Dalsgaard 2002; Engström et al. 2005) or marine OMZ waters (Dalsgaard et al. 2003; Kuypers et al. 2005). As more measurements were made, anammox rarely accounted for more than one third of estuarine N_2 production (Hietanen 2007; Hietanen and Kuparinen 2007; Rich et al. 2008; Koop-Jakobsen and Giblin 2009; Nicholls and Trimmer 2009; Dong et al. 2011; Crowe et al. 2012; Teixeira et al. 2012; Bernard et al. 2014; Lisa et al. 2015), suggesting that denitrification typically accounts for the bulk of N loss from these ecosystems. Some studies have found much higher contributions of anammox when using potential rate measurements (in which an overabundance of substrates are supplied; Crowe et al. 2012; Teixeira et al. 2012), suggesting that ammonium or nitrite may be limiting in situ anammox rates in some environments. This is logically consistent with the hypothesis of Koeve and Kähler (2010), which predicted that anammox rates should scale with ammonium availability; the measurements by Crowe et al. (2012) in the Lower Saint Lawrence Estuary appear to strongly support this hypothesis, as these sediments were electron-donor limited and thus highly dependent on OM remineralization. However, nitrite limitation may also occur in sediments, as numerous studies have found anammox rates positively correlated with nitrite or nitrate concentrations (with nitrate concentrations potentially affecting anammox by limiting nitrate reduction to nitrite; Trimmer et al. 2003; Engström et al. 2005; Meyer et al. 2005; Teixeira et al. 2012; Hou et al. 2013; Brin et al. 2014; Plummer et al. 2015; Teixeira et al. 2016).

As previously mentioned, one of the prime drivers of anammox compared with denitrification appears to be organic carbon availability. Because estuarine denitrification is predominantly heterotrophic, high organic carbon concentrations typically stimulate denitrification, which either suppresses anammox (due to competition for nitrite) or simply lowers the percent anammox due to constant anammox but massive denitrification rates. Many studies have found negative correlations between anammox rates and organic carbon content of sediments, suggesting that anammox may actually be suppressed in such eutrophic environments (Thamdrup and Dalsgaard 2002; Risgaard-Petersen et al. 2004b; Hietanen and Kuparinen 2007; Nicholls and Trimmer 2009; Jäntti et al. 2011; Brin et al. 2014; Plummer et al. 2015). In a counterintuitive twist, however, some studies have found positive correlations between sediment organic carbon content and anammox rates (Trimmer et al. 2003; Bale et al. 2014; Lisa et al. 2014; Lisa et al. 2015). These correlations are attributed to high rates of ammonium or nitrite production due to the enhanced heterotrophic remineralization (producing ammonium) and nitrification (stimulated by the high ammonium availability and producing nitrite), though it is unclear why denitrification in these systems was not concurrently stimulated.

Overall, while most studies of anammox in estuaries have suggested percent anammox less than 25% (Trimmer et al. 2003; Risgaard-Petersen et al. 2004b; Hietanen 2007; Rich et al. 2008; Dong et al. 2009; Koop-Jakobsen and Giblin 2009; Brin et al. 2014; Lisa et al. 2015; Bonaglia et al. 2016), estimates in some estuaries have reached nearly 80% (Engström et al. 2005; Teixeira et al. 2012). Additionally, percent anammox is often highly geographically variable within an estuary (Dong et al. 2009; Crowe et al. 2012; Teixeira et al. 2012; Brin et al. 2014). These conflicting results underscore the heterogeneity of estuaries, suggesting that certain environmental and biogeochemical factors may have drastically different effects between ecosystems.

Distribution of Anammox Bacteria in Estuaries

Because all known anammox bacteria belong to a relatively restricted set of genera within *Planctomycetales* (Kartal et al. 2011), 16S rRNA genes can be used to specifically target anammox bacteria in environmental samples (Schmid et al. 2000; Kuypers et al. 2003; Penton et al. 2006; Rich et al. 2008; Dale et al. 2009; Teixeira et al. 2012; Fernandes et al. 2016). Until recently, our relative ignorance of anammox biochemistry and genomics precluded the identification of useful functional gene markers (Francis et al. 2007). However, numerous functional genes have since emerged (Table 1): *Scalindua*-like *nirS* (Lam et al. 2009), which codes for a nitrite reductase specific to *Scalindua* bacteria, the dominant anammox bacteria in marine OMZs (Kuypers et al. 2003; Dalsgaard et al. 2005; Lam et al. 2009); *hzoAB* (Schmid et al. 2008; Hirsch et al. 2011), which codes for part of a hydrazine oxidase enzyme that oxidizes hydrazine (N_2H_4, an intermediate in the anammox pathway) to N_2 (Kartal et al. 2011), though the usefulness of this gene may be hindered by genomic evidence that some anammox bacteria have numerous divergent copies (Strous et al. 2006); and *hzsA* or *hzsB* (Harhangi et al. 2012; Wang et al. 2012b), coding for part of the novel hydrazine synthase enzyme that combines nitric oxide (NO) and ammonium to form hydrazine (Kartal et al. 2011). Many recent estuarine studies have studied anammox bacteria using a combination of 16S rRNA genes and either *hzo* or *hzs* (Hirsch et al. 2011; Li et al. 2011; Wang et al. 2012a; Bale et al. 2014; Naeher et al. 2015). Although many patterns in anammox bacterial diversity and abundance are present across estuaries, the clearest pattern is the shift in diversity along salinity gradients (Sonthiphand et al. 2014). The two dominant genera of anammox bacteria in estuaries

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are *Scalindua* and *Brocadia* (though other genera such as *Kuenenia*, *Anammoxoglobus*, and *Jettenia* are sometimes found as well). Sediments in freshwater estuarine regions are typically dominated by *Brocadia*-like bacteria, while marine sediments are mostly *Scalindua*-like (Teixeira et al. 2012; Wang et al. 2012a; Sonthiphand et al. 2014; Naeher et al. 2015; Fernandes et al. 2016). Sampling along a salinity gradient often gives a predictable shift between these two groups (Dale et al. 2009; Hirsch et al. 2011; Lisa et al. 2014; Zheng et al. 2016). Fewer studies have investigated seasonal changes in anammox bacterial diversity in estuaries, but some have shown substantial changes in anammox communities between seasons (Li et al. 2011; Wang et al. 2012a). Finally, while some estuarine studies have shown that anammox bacterial gene abundances (either 16S rRNA or functional genes) positively correlated to anammox rates (Bale et al. 2014; Lisa et al. 2014), the two are often unrelated, with high gene abundances even when anammox rates are low or undetectable (Hirsch et al. 2011; Wang et al. 2012a; Lisa et al. 2015; Naeher et al. 2015). Although anammox bacteria appear ubiquitous in estuary sediments, this suggests that their presence may not always be indicative of high activity.

DNRA: an Alternative Nitrate Shunt

DNRA Rates in Estuaries

An additional fate of nitrate respiration is the reduction to nitrite followed by nitrite reduction to ammonium, or "dissimilatory nitrate reduction to ammonium" (DNRA; Fig. 1). Although long recognized in bacterial cultures (Cole and Brown 1980; MacFarlane and Herbert 1982) and some environments (Keeney et al. 1971; Koike and Hattori 1978a; Sørensen 1978a), DNRA has only recently been brought to prominence in estuaries (Giblin et al. 2013): numerous recent studies have measured high benthic DNRA rates compared to denitrification or anammox (Tobias et al. 2001; An and Gardner 2002; Gardner et al. 2006; Koop-Jakobsen and Giblin 2010; Dong et al. 2011; Jäntti and Hietanen 2012; Song et al. 2014; Bernard et al. 2015; Hardison et al. 2015), suggesting that this process can play an important role in estuarine N cycling. Although DNRA, denitrification, and anammox all reduce oxidized N, denitrification and anammox lead to N_r loss from an ecosystem (via gaseous N production), whereas the N respired by DNRA is retained within the system as ammonium. Therefore, understanding the dynamics controlling DNRA rates (as well as its interactions with denitrification and anammox) is critical for understanding the fate of nitrogen in estuaries.

Studies to date suggest that many environmental processes may affect benthic DNRA rates (Burgin and Hamilton 2007; Giblin et al. 2013). Although DNRA has a lower energetic yield than denitrification (i.e., fewer ATP generated per molecule of substrate oxidized), it can accept a greater number of electrons per nitrate molecule (eight, compared to five for denitrification). For this reason, DNRA may be energetically favored over denitrification in anoxic environments where electron acceptors are limiting and electron donors (such as organic carbon or sulfide) are in excess, whereas denitrification would be favored when electron donors are limiting but nitrate is plentiful (Tiedje et al. 1982). This idea has been bolstered by evidence from culture experiments (Cole and Brown 1980; Kraft et al. 2014; van den Berg et al. 2015) as well as field data (King and Nedwell 1985; Dong et al. 2009; Porubsky et al. 2009; Dong et al. 2011; Hardison et al. 2015; Peng et al. 2016). Measurements in numerous estuaries have also suggested that DNRA can be correlated to temperature (Giblin et al. 2010; Smyth et al. 2013). Along these lines, Dong et al. (2011) found a dominance of DNRA over denitrification and anammox in samples from many tropical estuaries and posited that this pattern may be due to indirect effects of temperature on nitrate concentrations, as high summertime productivity often leads to nitrate depletion in the water column.

Other studies have found high DNRA rates in sediments with high concentrations of sulfide (Brunet and Garcia-Gil 1996; An and Gardner 2002; Gardner et al. 2006; Plummer et al. 2015), which can accumulate in anoxic estuarine or marine sediments as the by-product of sulfate reduction (Jørgensen et al. 1990). Importantly, sulfide inhibits nitrification (and thus coupled nitrification-denitrification; Joye and Hollibaugh 1995) and can also block the reduction of nitric oxide or nitrous oxide during denitrification (Sørensen et al. 1980). It is unclear whether high DNRA rates in sulfidic sediments are caused by an enhancement of DNRA coupled to sulfide oxidation (i.e., excess electron donor), or whether bacteria performing DNRA simply have a higher sulfide tolerance than nitrifiers and denitrifiers. It remains unknown whether positive correlations *always* exist between sulfide availability and DNRA, however, as some reports have suggested inhibition of DNRA at high sulfide concentrations (Porubsky et al. 2009; Roberts et al. 2014).

Finally, it is worth noting the recent discovery that diatoms can survive periods of dark anoxia by respiring nitrate via DNRA (Kamp et al. 2015). Although shoal sediments in many estuaries host ample populations of benthic diatoms in close proximity to anoxic sediments, no studies to date have explored the in situ ability of benthic diatoms to perform DNRA in estuary sediments. Given their ubiquity in some ecosystems, however, this process could potentially exert a significant effect on benthic N cycling in some estuaries.

Microbial Ecology of DNRA

DNRA can be coupled to heterotrophic (fermentative) carbon oxidation or to chemolithoautotrophic growth via sulfur

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oxidation (Tiedje 1988; Brunet and Garcia-Gil 1996). A broad variety of microbes are capable of DNRA, including *Firmicutes*, *Verrucomicrobia*, *Planctomycetes*, *Acidobacteria*, *Chloroflexi*, *Chlorobia*, and many classes of *Proteobacteria* (Tiedje 1988; Welsh et al. 2014). Like denitrification, this diversity limits the utility of 16S rRNA data for exploring the microbial ecology of DNRA in the environment. However, functional gene analyses have proved fruitful. Following the reduction of nitrate to nitrite via a periplasmic nitrate reductase (Nap), nitrite is reduced to ammonium by a unique periplasmic cytochrome *c* nitrite reductase (Nrf). This latter enzyme is encoded by the *nrfA* gene (Darwin et al. 1993; Einsle et al. 2000), which has become a useful marker gene for DNRA in the environment (Table 1; Mohan et al. 2004; Welsh et al. 2014).

Compared to other N-cycling microbes, there are relatively few studies of the community dynamics of DNRA bacteria in estuaries. Diversity of *nrfA* in estuaries is high and often changes along salinity gradients (Takeuchi 2006; Smith et al. 2007; Song et al. 2014; Decleyre et al. 2015). Pyrosequencing of the *nrfA* gene along the New River estuary (NC, USA) suggested that DNRA bacterial communities were dominated by a relatively small number of abundant ecotypes (similar to benthic denitrifiers, as discussed above), though phylogenetic diversity among these abundant ecotypes was high and there were also endemic populations at each site (Song et al. 2014); these data also suggested a number of OTUs from known sulfur-oxidizing genera present only in sulfide-rich sediments, suggesting that DNRA in these regions may be stimulated by high sulfide concentrations. Abundance of *nrfA* genes was highest in the New River estuary at brackish sites with high benthic organic C content, a pattern also seen in oyster bed sediments (Song et al. 2014; Lindemann et al. 2016). Work in the Colne estuary (UK) showed correspondences between *nrfA* gene abundances and DNRA rates, with highest abundances and rates in the brackish/fresh regions of the estuary, although patterns of *nrfA* transcripts were more complex (Smith et al. 2007; Dong et al. 2009; Smith et al. 2015a). The enormous diversity of DNRA bacteria in estuaries and the relatively small number of studies on their distributions clearly warrants further study, particularly given the evidence of the importance of DNRA in the N cycle of many estuaries.

Nitrification: Transferring Reduced N to the Oxidized N_r Pool

Ammonia and Nitrite Oxidation Link N Inputs and Outputs

Nitrification is the microbially catalyzed oxidation of ammonia to nitrite and nitrate (Fig. 1) and is the only known aerobic pathway for oxidizing ammonia in the environment (Ward 2008) and thus linking the reduced N produced by remineralization to the oxidized substrates (nitrite and nitrate) required for the N-loss processes. As such, nitrification is the sole link between OM inputs and N_r removal and therefore is a critical link in the estuarine N cycle.

Because nitrification is an aerobic metabolism and therefore simpler to measure in the field compared to anaerobic processes, measurements of nitrification rates in estuaries are relatively prolific. Nitrification can occur in both the sediments and the water column of estuaries, provided that oxygen is available (Fig. 1). If nitrifying activity is high enough (e.g., in sediment slurries), changes in nitrite or nitrate concentrations during incubations can be used to calculate nitrification rates. When activity is lower, stable isotope (^{15}N) incubations can be used to measure nitrification, either by adding $^{15}N–NH_4^+$ as a tracer and measuring the accumulation of ^{15}N-labeled nitrite and nitrate (NO_X), or by adding $^{15}N–NO_X$ and measuring the subsequent "dilution" of the NO_X pool by newly produced $^{14}N–NO_X$. Many studies have also measured carbon fixation (since both ammonia and nitrite oxidizers are autotrophic) or changes in nutrient concentrations in parallel incubations with and without nitrification inhibitors (Table 1). Below, we summarize trends in nitrification rates both in the water column and sediments of estuaries.

Nitrification Rates in Estuary Waters

Water column nitrification rates show a wide range between estuarine ecosystems, but are often greater than the rates typical of shallow or open ocean waters, where nitrification rarely exceeds ~ 50 nM day^{-1}(e.g., Dore and Karl 1996; Beman et al. 2008; Santoro et al. 2010; Newell et al. 2013); for a detailed discussion and compilation of data on estuarine water column nitrification rates, see Damashek et al. (2016). Nitrification is often high in estuary waters downstream of ammonium sources (e.g., sewage outfalls), leading to strong correlations between nitrification rates and ammonium concentrations (Somville 1984; Lipschultz et al. 1986; Iriarte et al. 1996; Brion et al. 2000; Damashek et al. 2016; McLaughlin et al. 2017). However, high nitrification rates have been measured in many estuarine waters with relatively low ammonium concentrations as well (Feliatra and Bianchi 1993; Bianchi et al. 1994; Pakulski et al. 1995; Bianchi et al. 1999; Pakulski et al. 2000; Carini et al. 2010; Bronk et al. 2014; Hsiao et al. 2014; Bristow et al. 2015; Heiss and Fulweiler 2016; Tolar et al. 2016), suggesting a tight coupling between ammonium production and oxidation in these systems. In fact, when nitrification and ammonium regeneration rates are measured simultaneously, high rates of both processes are often found to occur in the same regions (Pakulski et al. 1995; Bronk et al. 2014). These contrasting scenarios indicate that nitrification can either be stimulated by allochthonous ammonium inputs or tightly linked to autochthonous ammonium production in estuarine waters.

In numerous estuaries, nitrification rates are elevated in particle-rich "estuary turbidity maxima" (ETMs; Helder and De

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Vries 1983; Owens 1986; Berounsky and Nixon 1993; Iriarte et al. 1996; Brion et al. 2000; de Wilde and de Bie 2000; Pakulski et al. 2000; Hsiao et al. 2014; Damashek et al. 2016). High nitrification is found in waters with various sources of turbidity, including both "classical" low-salinity ETMs and river plumes. Due to the trapping of OM, ETMs typically have high rates of microbial activity and biogeochemical cycling (Crump and Baross 1996; Goosen et al. 1999), and river plumes are enriched in allochthonous OM (Benner and Opsahl 2001). High microbial activity and biogeochemical activity (and therefore organic N remineralization to ammonium) likely drive high nitrification in these waters. In his seminal study of the Tamar Estuary, Owens (1986) described correlations between nitrification and turbidity as a "fluidized bed reactor," with resuspension of benthic nitrifiers into the oxic, ammonium-rich water column alleviating oxygen limitation experienced by benthic nitrifiers in surface sediments and thus leading to high nitrification rates. Alternatively, high nitrification could be due to stimulation of water column ammonia oxidizers by abiotic ammonium release during sediment resuspension, such as advection of porewater ammonium or desorption of ammonium from sediment particles, which can increase ammonium availability during resuspension events (Fitzsimons et al. 2006; Percuoco et al. 2015; Wengrove et al. 2015). While nitrification and turbidity are clearly correlated across a wide range of estuaries, understanding the mechanistic cause of this relationship is still an open question.

In estuaries with hypoxic or anoxic waters, nitrification often peaks at the oxic-anoxic interface (McCarthy et al. 1984; Enoksson 1986; Ward and Kilpatrick 1990; Iriarte et al. 1998; Hietanen et al. 2012; Urakawa et al. 2014; Berg et al. 2015). Enhanced oxycline nitrification is often attributed to ephemeral mixing between ammonium-enriched deeper waters with oxygen-rich shallower waters, which creates temporary patches where both ammonium and oxygen are available (Horrigan et al. 1990; Berg et al. 2015). This hypothesis is similar to the concept of sediment-water mixing stimulating nitrification in the water column (Owens 1986) discussed above: nitrifiers in low-oxygen environments are likely oxygen-limited while those in most oxygenated waters are ammonia-limited, but mixing between the two can alleviate both limitations and thus lead to high nitrification rates. While nitrification is often high in hypoxic waters, rates measured from the anoxic zone of the Baltic Sea and in anoxic incubations from the Gulf of Mexico show low or undetectable rates when no oxygen is present (Berg et al. 2015; Bristow et al. 2015). It is worth noting that high nitrification rates have been reported from the oxic-anoxic transition zones at the edges of oxygen minimum zones (OMZs) in the ocean (Beman et al. 2008; Newell et al. 2011), and high abundance or transcriptional activity of ammonia-oxidizing microorganisms have also been documented at OMZ edges and estuary pycnoclines (Beman et al. 2008; Newell et al. 2011; Stewart et al. 2012; Hewson et al. 2014). Additionally, culture-based studies of the ammonia-oxidizing archaeon *Nitrosopumilus maritimus* SCM1 have demonstrated a remarkably high affinity for both ammonium and oxygen (Martens-Habbena et al. 2009), suggesting at least some ammonia-oxidizing archaea can respond rapidly to the availability of either substrate.

Finally, temperature is positively correlated with nitrification rates in many estuaries (Somville 1978; Berounsky and Nixon 1990; Berounsky and Nixon 1993; Iriarte et al. 1998; Bianchi et al. 1999; de Bie et al. 2002; Gazeau et al. 2005; Dai et al. 2008; Miranda et al. 2008; Damashek et al. 2016). Due to high microbial respiration at high temperatures (e.g., White et al. 1991; Caffrey 2004), high nitrification in summer could be due to high ammonium regeneration or could simply be due to higher growth rates of nitrifiers at higher temperatures. Recent experimental evidence from Sapelo Island waters showed a decoupling of ammonia and nitrite oxidation at warm temperatures (20–30 °C), with greater stimulation of ammonia oxidation leading to a buildup of nitrite during summer (Schaefer and Hollibaugh 2017); in the same study, a meta-analysis of nitrite data showed a stronger relationship between high nitrite concentrations and temperature as compared to other environmental factors (including oxygen and ammonium), suggesting a direct link between temperature and nitrite in many temperate coastal ecosystems. While activity was highest in summer in many estuaries, other coastal and estuarine regions had nitrification rates that peaked in winter (Christman et al. 2011; Baer et al. 2014), suggesting that positive correlations with temperature are not universal.

Benthic Nitrification Rates in Estuaries

Due to relative ease and low cost, a common method of estimating nitrification rates in sediments is measuring potential rates using ammonium-amended slurries shaken (i.e., aerated) in the dark at room temperature (Hansen et al. 1981; Kemp et al. 1990; Dollhopf et al. 2005; Damashek et al. 2015; Smith et al. 2015b). Using this method, nitrification occurs so rapidly that changes in nitrate plus nitrite (NO_X) concentrations can be measured with standard colorimetric techniques following relatively short incubation times (often 6 to 24 h), alleviating the need to use ^{15}N tracers. However, potential rates are not necessarily reflective of in situ nitrification rates, due to the removal of any limitations imposed by substrate/oxidant availability, temperature, or light. Furthermore, potential nitrification rates may actually be lower than in situ rates, such as when necessary geochemical/redox gradients [e.g., O_2, hydrogen sulfide (H_2S), etc.] are disturbed, leading to suboptimal or inhibitory conditions (see H_2S discussion below; Dollhopf et al. 2005). Even so, these measurements are a useful tool to compare biogeochemical rates of nitrifying microbial communities from different samples.

For estimating in situ nitrification rates, methods used with sediment cores are similar to those used to measure water

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column nitrification, including measuring radioactive (^{14}C) bicarbonate uptake or NO_X production in the presence of nitrification inhibitors (Henriksen 1980; Sloth et al. 1992; Caffrey and Miller 1995) or using $^{15}NH_4^+$ tracers to track ammonium oxidation to $^{15}NO_X$ (Binnerup et al. 1992; Rysgaard et al. 1996; Wankel et al. 2011). Tracer methods, though not without their own assumptions (e.g., homogeneous mixing of tracers, knowledge of isotope effects for multiple processes, minimal recycling of labeled compounds during the incubation), can give reasonable estimates of in situ nitrification rates and, if $^{15}N_2$ is measured, coupled nitrification-denitrification rates (Nielsen 1992), which can be a particularly important nitrogen loss process in estuary sediments (Jenkins and Kemp 1984).

The most common environmental parameter affecting benthic nitrification rates in estuaries is productivity, though correlations between productivity and nitrification can be either positive or negative. Primary productivity has direct effects on nitrification due to photosynthetic ammonium uptake and oxygen production: because nitrification requires both ammonium and oxygen, high primary productivity can either stimulate nitrification by providing oxygen or inhibit nitrification due to direct competition for ammonium. Competition is particularly important in sediments with active benthic microalgae, which typically outcompete ammonia oxidizers for available ammonium and thus suppress nitrification (Rysgaard et al. 1995; Risgaard-Petersen 2003; Risgaard-Petersen et al. 2004a). Phytoplankton growth can inhibit ammonia oxidation in coastal ocean waters, as well (Smith et al. 2014). Conversely, when ammonium is abundant in porewaters, photosynthetic oxygen production can directly stimulate nitrification (Sloth et al. 1992; Gao et al. 2012).

Indirect effects of productivity can also either stimulate or depress nitrification. Periods of high primary productivity are typically followed by OM deposition and high benthic respiration, with labile organic N rapidly remineralized to ammonium; therefore, high productivity followed by remineralization can lead to a large injection of "new" ammonium into surface sediments, which can stimulate nitrification (if oxygen is available). However, because oxygen is rapidly consumed during respiration, oxygen penetration in OM-rich sediments is often reduced to a narrow surface layer (a few millimeters deep), minimizing the zone where nitrification can occur. Additionally, this rapid microbial activity often drives brackish and marine sediments to a regime where oxygen and nitrate are rapidly consumed and high rates of sulfate reduction, and thus sulfide accumulation, occur close to the sediment surface (Jørgensen and Sørensen 1985). Because sulfide can inhibit nitrification (Joye and Hollibaugh 1995), the resulting buildup of porewater sulfide in highly productive sediments can severely inhibit nitrification (Sloth et al. 1995; Rysgaard et al. 1996). Dollhopf et al. (2005) provided an elegant illustration of this effect in coastal salt marsh sediments off the Georgia (USA) coast: potential nitrification rates were not only inversely correlated to sulfide concentrations but also positively correlated to ferric iron [Fe(III)]. Because Fe(III) rapidly oxidizes H_2S to (less toxic) elemental sulfur, and Fe(II) can further react with H_2S to form FeS (Canfield et al. 1992), high Fe(III) in these sediments effectively alleviated repression of nitrification by sulfide.

In addition to potentially explaining correlations between nitrification rates and the parameters suggested above, effects of productivity on nitrification are often reflected by correlations between benthic nitrification and water temperature, either positive (due to high concentrations of remineralized ammonium or photosynthetically produced oxygen, as discussed above, or due to stimulation of nitrifier growth rates; Henriksen et al. 1981; Caffrey et al. 1993; Caffrey and Miller 1995; An and Joye 2001; Usui et al. 2001; Caffrey et al. 2003; Smith et al. 2015b) or negative (due to stimulation of heterotrophs and the resulting oxygen depletion), with low nitrification rates in summer (Hansen et al. 1981; Nedwell et al. 1983; Jenkins and Kemp 1984; Kemp et al. 1990; Sloth et al. 1992; Caffrey et al. 2003; Bernhard et al. 2007; Tait et al. 2014; Li et al. 2015; Lisa et al. 2015). Studies from multiple estuaries have shown that relatively small OM additions stimulate nitrification rates, but only to a point; past this threshold, further eutrophication causes nitrification to plummet due to oxygen depletion (particularly in estuaries with stagnant waters; Caffrey et al. 1993, 2003; Magalhães et al. 2005; Wankel et al. 2011). In this way, responses to "new" ammonium sources are highly dependent on oxygen availability. Taken together, the multifactorial effects of productivity on nitrification are likely one of the sources of heterogeneity in benthic N biogeochemistry between ecosystems and underscore the importance of comparing the drivers of nitrification between many estuaries.

Other than the direct and indirect effects of productivity, another common factor influencing benthic nitrification rates is macrofaunal activity. As these animals (e.g., clams, worms, etc.) move their physical activity can mix surface sediment layers, and their burrows allow bottom waters to move through the sediments, ventilating the benthos with oxygen (and other dissolved nutrients; Meysman et al. 2006). Similar to the discussion above, this addition of "new" oxygen to the sediments can stimulate nitrification. Although not always directly quantified, the pattern of high nitrification rates in regions with dense macrofaunal populations has been documented across numerous estuaries (Kristensen et al. 1985; Caffrey and Miller 1995; Mayer et al. 1995; Pelegrí and Blackburn 1995; Rysgaard et al. 1995; Usui et al. 2001; Eriksson et al. 2003; Caffrey et al. 2016).

Microbial Ecology of Ammonia and Nitrite Oxidizers

Historically, nitrification was believed to only occur in two steps: ammonia oxidation to nitrite by ammonia oxidizers

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and further oxidation of nitrite to nitrate by a distinct group of nitrite-oxidizing bacteria (NOB). Recently, some *Nitrospira* bacteria were shown to completely oxidize ammonia to nitrate in one step, a completely novel "comammox" (complete ammonia oxidation) metabolism (Daims et al. 2015; van Kessel et al. 2015). To date, however, the presence of comammox bacteria has not been demonstrated in estuaries; we therefore restrict our discussion of nitrification to "canonical" ammonia and nitrite oxidizers.

For well over a century (Winogradsky 1890), the only microbes known to oxidize ammonia were a few genera within the *Betaproteobacteria* (*Nitrosomonas* and *Nitrosospira*) and *Gammaproteobacteria* (*Nitrosococcus*). Due in part to the phylogenetically restricted nature of this functional guild, the *amoA* gene, coding for the α-subunit of the ammonia monooxygenase enzyme, became a robust functional gene for studying these ammonia-oxidizing bacteria (AOB) in the environment (Rotthauwe et al. 1997; Kowalchuk and Stephen 2001). However, just over a decade ago, this paradigm was overturned by the discovery of ammonia-oxidizing archaea (AOA). Early PCR clone libraries of 16S rRNA genes from coastal ocean waters led to the discovery of two groups of mesophilic marine archaea, including a ubiquitous clade of mesophilic *Crenarchaeota* called Marine Group I (MGI) *Crenarchaeota* (DeLong 1992; Fuhrman et al. 1992), which were later shown to be highly abundant in the deep ocean (Karner et al. 2001). Following years of work characterizing the diversity and metabolic lifestyles of these archaea (e.g., MacGregor et al. 1997; Ouverney and Fuhrman 2000; Wuchter et al. 2003), putative archaeal *amoA* sequences were discovered in both oceanic and soil metagenomes (Venter et al. 2004; Treusch et al. 2005), suggesting that MGI *Crenarchaeota* may be capable of oxidizing ammonia. The first pure culture of this group of archaea, *Nitrosopumilus maritimus* SCM1 (Könneke et al. 2005), confirmed the hypothesis of chemoautotrophic growth via aerobic ammonia oxidation. In the past decade, numerous other strains of aquatic AOA have been isolated from cosmopolitan environments including estuary sediments (Blainey et al. 2011; Mosier et al. 2012a, b, c), marine sediments (Park et al. 2010, 2014), the marine water column (Santoro et al. 2015; Bayer et al. 2016; Ahlgren et al. 2017), and lake sediments (French et al. 2012), among others. Comparative genomics has suggested that MGI *Crenarchaeota* are representative of a distinct phylum, designated the *Thaumarchaeota* (Brochier-Armanet et al. 2008; Pester et al. 2011).

Initial studies sequencing environmental AOA *amoA* genes showed partitioning of diversity by habitat, including clades distinctive of terrestrial soils, the marine water column, and low-salinity regions (Francis et al. 2005). Quantitative analyses of ammonia-oxidizing populations suggested that AOA vastly outnumbered AOB in many environments (Leininger et al. 2006; Wuchter et al. 2006; Caffrey et al. 2007; Francis et al. 2007; Beman et al. 2008; Santoro et al. 2010). Despite the high relative abundance of AOA (compared to AOB) in many ecosystems, estuary sediments confounded this early pattern: while some estuaries do have abundant AOA populations (Caffrey et al. 2007; Moin et al. 2009; Abell et al. 2010; Bernhard et al. 2010; Jin et al. 2011; Peng et al. 2013), others are dominated by AOB (Magalhães et al. 2009; Wankel et al. 2011; Abell et al. 2013; Li et al. 2015), and some have geographically variable patterns of relative abundance (Mosier and Francis 2008; Santoro et al. 2008; Bouskill et al. 2012; Zheng et al. 2014; Smith et al. 2015b). Links between microbial community structure and biogeochemical function also vary substantially between estuaries: of the relatively few studies simultaneously measuring sediment nitrification rates (often measured as potential rates) in combination with ammonia oxidizer abundances, some have found correlations between rates and AOA abundances (Caffrey et al. 2007; Bowen et al. 2014), while others showed a strong correspondence between AOB abundances and rates (Bernhard et al. 2007; Damashek et al. 2015; Smith et al. 2015b); however, correlations between rates and gene abundances are not always apparent (Bernhard et al. 2010; Li et al. 2015). Therefore, it is not always straightforward to ascertain whether AOA or AOB are the main drivers of nitrification in any particular estuary based on gene abundances.

AOA diversity in some environments, including the marine water column and soils, is relatively restricted, with only a small number of well-defined clades typically represented (Francis et al. 2005; Prosser and Nicol 2008; Biller et al. 2012; Pester et al. 2012). In estuaries, however, their diversity is more complex (Bernhard and Bollmann 2010). Ammonia oxidizer diversity in the well-studied estuarine benthos includes sequences from common "soil" and "marine" clades as well as the broader "sediment" clades, as defined by Francis et al. (2005) (Biller et al. 2012), and a distinct "low salinity" clade (Mosier and Francis 2008). In addition to high levels of diversity in estuary sediments as a whole, geographic partitioning of AOA *amoA* diversity often occurs along the salinity gradient; marine ends of many estuaries often contain abundant sequences from "sediment" clades (including *Nitrosopumilus*- and *Nitrosotenuis*-like clades) and occasionally (but rarely) sequences from the marine water column clades, whereas freshwater regions of estuaries often contain *Nitrosoarchaeum*-like (i.e., the "low salinity" clade) and group 1.1b AOA (the "soil" clade, perhaps indicative of terrestrial influences), with *Nitrosopumilus*-like sequences also common in brackish sediments (Francis et al. 2005; Beman and Francis 2006; Dang et al. 2008; Mosier and Francis 2008; Sahan and Muyzer 2008; Bernhard et al. 2010; Wankel et al. 2011; Damashek et al. 2015; Smith et al. 2015b).

Similar to AOA, the diversity of AOB *amoA* genes in estuary sediments typically varies along the estuary salinity

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gradient (Francis et al. 2003; Bernhard et al. 2005; Beman and Francis 2006; Freitag et al. 2006; Mosier and Francis 2008; Sahan and Muyzer 2008; Santoro et al. 2008). AOB communities in most estuaries are not as diverse as AOA communities, with most *amoA* sequences falling into a limited number of *Nitrosomonas*-like and *Nitrosospira*-like clades (Nicolaisen and Ramsing 2002; Caffrey et al. 2003; Beman and Francis 2006; Moin et al. 2009; Wankel et al. 2011; Peng et al. 2013). In addition, some estuarine AOB communities appear to differ between regions with low and high N loading (Dang et al. 2010; Wankel et al. 2011; Peng et al. 2013; Damashek et al. 2015), which is particularly interesting in light of the fact that AOB are often the dominant ammonia oxidizer within aerated nitrifying wastewater treatment plants (WWTPs; e.g., Wells et al. 2009), suggesting that some AOB may be adapted to live at high nutrient conditions in estuary sediments, as well.

Ammonia-oxidizing communities in estuary water columns are vastly understudied compared to estuary sediments. However, a few studies have documented distinct pelagic populations in different salinity regimes, similar both to benthic ammonia-oxidizing communities (see above) and the overall microbial community in estuary waters (e.g., Bouvier and del Giorgio 2002; Crump et al. 2004; Herlemann et al. 2011; Fortunato et al. 2012; Campbell and Kirchman 2013). An early study of the Elbe river estuary found a decrease in AOB abundances in saline regions, with *Nitrosomonas*-like sequences abundant in clone libraries from across the estuary (Stehr et al. 1995). Studies in the Seine River Estuary and the Scheldt found dramatic shifts in AOB community diversity between freshwater regions (mostly *Nitrosomonas*-like) and saltier regions (mostly *Nitrosospira*-like), and distinct populations in freshwater regions receiving WWTP effluent (Speksnijder et al. 1998; de Bie et al. 2001; Cébron et al. 2003, 2004). Since the discovery of AOA, only a few studies have compared AOA and AOB in estuary waters. While AOA outnumber AOB in across the Changjiang estuary (including a shift from *Nitrosopumilus*-like AOA in freshwater regions compared to marine water column clades in marine regions; Zhang et al. 2014), relative abundances in the Chesapeake Bay differed by region, with nearly equal abundance of AOA and AOB in freshwater regions but a predominance of AOA (including *Nitrosopumilus*-like clades and marine water column A) near the estuary mouth (Bouskill et al. 2012). The general paucity of data comparing AOA and AOB in estuary waters warrants further study in different ecosystems to ascertain the drivers of these communities, as well as whether any inter-ecosystem patterns exist.

In one of the only studies quantifying abundances of both ammonia and nitrite oxidizers in estuary waters, Cébron et al. (2003) found that abundances of both AOB and NOB were highest in the Seine River estuary downstream of a massive input of WWTP effluent, and both were correlated with potential nitrification activity. In perhaps the only study investigating benthic *and* pelagic ammonia and nitrite oxidizers in an estuary, Helder and de Vries (1983) found far greater abundances of AOB in sediments of the Ems-Dollard estuary (Germany/the Netherlands) using the most probable number (MPN) technique, suggesting that benthic populations may have a greater contribution to biogeochemical cycling in the estuary. Although they were unable to enrich NOB from the water column of the estuary, NOB were present in sediments, suggesting that the AOB/NOB population dynamics (combined with differential affinities for oxygen) led to a mid-estuary peak in nitrite (Helder and De Vries 1983). It is unfortunate that few studies have been conducted on nitrite-oxidizing populations in estuaries, given the relative wealth of knowledge on estuarine ammonia oxidizers. This may be largely due to the lack of NOB-specific functional gene markers as effective as *amoA*; due to the high divergence of *nxr* genes (encoding the nitrite oxidoreductase enzyme) between the different genera of NOB, no single primer set has been designed that can capture the full spectrum of NOB (e.g., *Nitrospira*, *Nitrospina*, *Nitrobacter*, etc.) commonly found in the environment, with each set instead focusing on one specific genus (e.g., Poly et al. 2008; Pester et al. 2014).

Both functional gene analyses and studies using metagenomics, metatranscriptomics, or metaproteomics in estuary waters have found evidence of substantial AOA populations at the marine end of estuaries (Hollibaugh et al. 2011; Smith et al. 2013; Fortunato and Crump 2015; Tolar et al. 2016), in turbid river plumes (Satinsky et al. 2014), and at oxic-anoxic interfaces (Labrenz et al. 2010; Feike et al. 2011; Tolar et al. 2013; Hewson et al. 2014; Colatriano et al. 2015). High AOA abundances in hypoxic estuary waters are comparable to the edges of marine OMZs, where AOA drive high nitrification rates (e.g., Beman et al. 2012; Ganesh et al. 2015). When these regions are sampled with significant depth resolution, distinct AOA communities are present at different depths and are often most abundant in hypoxic (but not suboxic) waters (Tolar et al. 2013; Berg et al. 2015; Bristow et al. 2015). Additionally, while nitrification rates are often high, ammonia oxidizers in these waters appear to be more tolerant of low oxygen than nitrite oxidizers, leading to the accumulation of newly produced nitrite (Bristow et al. 2015), as also demonstrated in enrichments from aerobic estuary waters (Helder and De Vries 1983). In some coastal waters, AOA populations dramatically fluctuate seasonally: in the turbid but oxic coastal waters at Sapelo Island (Georgia, USA), dense blooms of AOA were first discovered in metatranscriptomes and have since been shown to reoccur every summer, though different phylotypes can be dominant during different years; while this bloom is generally largest during periods of high net heterotrophy, the mechanistic understanding of its dynamics is still unclear (Hollibaugh et al. 2011; Hollibaugh et al. 2014). In contrast, AOA abundance in some other coastal regions

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(e.g., the coastal Arctic and North Sea) peaks in winter (Christman et al. 2011; Pitcher et al. 2011). Clearly, there is still much to be learned about the seasonal drivers of AOA populations in these ecosystems.

Conclusions and Knowledge Gaps

Studies of N cycling in estuaries have proliferated in recent years, due in part to technological advances in both microbial ecology and biogeochemistry. As urbanization and development on their shores and in their watersheds accelerates in coming years, the ecosystem stresses imposed by anthropogenic nutrient pollution in estuaries are likely to increase, underscoring the importance of understanding the controls on N cycling processes. The diversity and complexity of estuaries preclude generalizing the conclusions from any single study across ecosystems, but many common trends are evident when the estuarine N cycling literature is examined as a whole.

Not surprisingly, environmental processes affecting oxygen cycling have significant impacts on N cycling in estuaries. However, the dynamics governing these relationships are complex and appear to depend on other factors such as nutrient loading as well. For example, high rates of primary productivity can drive both oxygen production (from photosynthesis) and ammonium production (as newly produced OM is remineralized), stimulating nitrification and coupled nitrification-denitrification. Yet, rampant primary productivity can also lead to rapid heterotrophic oxygen consumption, which cannot only deprive nitrifiers of oxygen but also lead to sulfide accumulation, either of which can suppress nitrification (and therefore denitrification as well). Direct competition between photosynthetic organisms and nitrifiers for available ammonium can also suppress nitrification rates. Finally, oxygen-nitrogen dynamics have come into focus for many N cycling pathways in relation to benthic macrofaunal abundance, as animal burrowing and excretion can ventilate sediments and transport nutrients between sedimentary layers and the water column. Understanding how N cycling microbes respond to changes in oxygen availability is clearly critical for understanding estuarine N cycling, but the complexity of these interactions precludes the generation of simple general models. Pairing field surveys with experimental manipulations and biogeochemical models in a diverse suite of estuaries is needed to tease out the effects of oxygen cycling processes on the estuarine N cycle.

The importance of considering nutrient stoichiometry as a driver of many N cycling processes is becoming evident. For example, while early hypotheses regarding the balance between denitrification and anammox focused on organic C or ammonium availability, recent work has demonstrated that the ratio between these substrates is often the controlling factor. Similarly, DNRA appears to often depend on the balance between electron donor (sulfide or organic C) and nitrate availability, and nitrification rates are only stimulated by increased ammonium availability if oxygen is available, as well. These patterns underscore the importance of taking a holistic view of estuarine biogeochemistry, instead of focusing on single environmental controls.

Overall, the majority of biogeochemical studies have focused on the benthos, with relatively few measurements of N cycling processes in the water column. For instance, the number of measurements of benthic remineralization dwarfs those made in the water column, despite the fact that pelagic microbial respiration is known to be high in many estuaries. Understanding rates of water column processes such as remineralization and nitrification is crucial for determining the extent of organic N processing prior to export to sediments or out of the estuary. Additionally, very few measurements of denitrification, anammox, or DNRA have been made in the water column of anoxic estuaries, but recent microbial data suggest that the populations catalyzing these reactions may be highly active in some estuarine waters. Sediments are often assumed to be hotspots of N cycling activity in estuaries, due to high OM and porewater nutrient concentrations. While microbial populations and biogeochemical reactions may indeed be higher in a fixed volume of sediment compared to the same volume of water, the total volume of the water column in many estuaries is larger than the total volume of biogeochemically active surface sediments, suggesting that integrated rates of water column processes play an important role in the biogeochemical function of the ecosystem. More work is needed to determine the contribution of benthic and pelagic processes to the overall N budget of estuaries, and to identify links between processes active in these two regimes.

Studies of N cycling microbial communities are often limited by the utility of functional genes for specific processes. Functional genes for N oxidation pathways, such as the *hzo*/*hzs* genes and archaeal *amo* genes used to study anammox bacteria and ammonia-oxidizing archaea, respectively, are often both unique/specific to the relevant microbial lineages and also provide enough phylogenetic information to describe their diversity. Ironically, these microbes are also restricted to specific phylogenetic lineages (within the *Planctomycetes* and *Thaumarchaeota* phyla) and can therefore be studied using 16S rRNA genes. Unfortunately, processes where N reduction is coupled to oxidation of other compounds (denitrification and DNRA) are both widespread phylogenetically and not usually the exclusive metabolism of the relevant microbes, precluding the sole use of 16S rRNA genes *and* potentially hampering the utility of functional genes. For example, because many "facultative" denitrifiers or DNRA bacteria can also grow via aerobic respiration (and sometimes other forms of anaerobic metabolism), the presence of *nir* or *nrf* genes in the environment does not necessarily mean these

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N-cycling processes are active. For these reasons, studying the microbial populations responsible for some N cycling pathways (e.g., ammonia oxidation) is much more straightforward than studying others (e.g., denitrification). Importantly, many of the N cycling microbes commonly found in estuaries are not closely related to any cultivated strains, limiting our understanding of their biochemistry or metabolic capabilities and also highlighting the need for novel approaches for isolating "ecologically-relevant" estuarine microbes.

Finally, while the number of studies investigating biogeochemical rates and microbial communities in estuaries has exploded in recent years, methods linking these two sources of data are still in their infancy (e.g., Coles and Hood 2016). In those studies where both types of data are collected, most attempts at data synthesis use pairwise correlations or relatively simple regression models, which are likely far too simple to adequately capture the complexity of these systems. Linking physical transport models with biogeochemical and microbial data is also likely necessary in order to properly scale up the measurements of biogeochemical rates or microbial communities to ecosystem scales. Clearly, much will be gained from interdisciplinary modeling efforts incorporating physical, biogeochemical, and microbial data to understand the estuarine N cycle.

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